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SCIENTIFIC AMERICAN

THE STORY OF US

IT'S STRANGER THAN ANYONE THOUGHT

— *INSIDE* —

- How climate shaped evolution
- Did we mate with Neandertals?
- Why humans must stay active to be healthy
- When we survived a near extinction
- The origins of language and culture

FALL 2019

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FROM THE EDITOR

Humanity's Journey

Around 195,000 years ago our planet entered a long glacial period known as Marine Isotope Stage 6. Cold, dry and harsh conditions settled in, and the number of *Homo sapiens* plummeted. A small remaining population eked out a living in southern Africa—one of the last habitable terrains. As Curtis W. Marean writes on page 24, DNA evidence shows that all humans are descended from that relatively small group of survivors (perhaps only several hundred individuals). We tend to think of humans as being evolutionary powerhouses who quickly and fiercely displaced all other hominin species. But this and other research reveal that humans actually often flirted with extinction. The more fossils that scientists find, and the better DNA-extraction techniques become, the more surprises they uncover.

Take our own origin story. Contrary to previous hypotheses, our family tree is quite the tangled mess of interbreeding species (*page 4*). New genetic identification techniques can now use small fragments of fossils to determine the parentage of hybrid species (*page 48*). And although human ingenuity evolved perhaps hundreds of thousands of years earlier than first estimated (*page 16*), we weren't the only hominins using symbolic art or creative thinking (*page 88*).

No other species has spread as far worldwide or evolved such an advanced communication system and cultural fabric (*page 56*). Humans are distinct from other creatures down to our brain makeup—with especially enlarged cortical regions associated with creativity and abstract thinking (*page 70*). Our use of language (*page 64*), our trust in one another (*page 74*), the way we dance (*page 92*) and even our (lack of) body hair are distinctly human (*page 80*) and have enabled us to thrive.

Where will these unique characteristics take us? Our future selves will likely be a vivid mosaic of skin tones and other physical features (*page 104*), although we may devise sophisticated technological avatars that interact with other virtual humans on our behalf (*page 99*). Perhaps we will send our genes out into the stars, to settle other planetary bodies or build stations in deep space itself (*page 110*).

But Earth will always be our first home. That we did not go extinct all those years ago is a testament to our resilience, as well as a warning: we are intricately tied to our environment. Indeed, climate data are revealing that human adaptability itself arose from the need to survive a changing planet (*page 10*). Humanity's story is a feedback loop of challenge and triumph, one that has brought us further than any other species we know of but whose end is not yet written.

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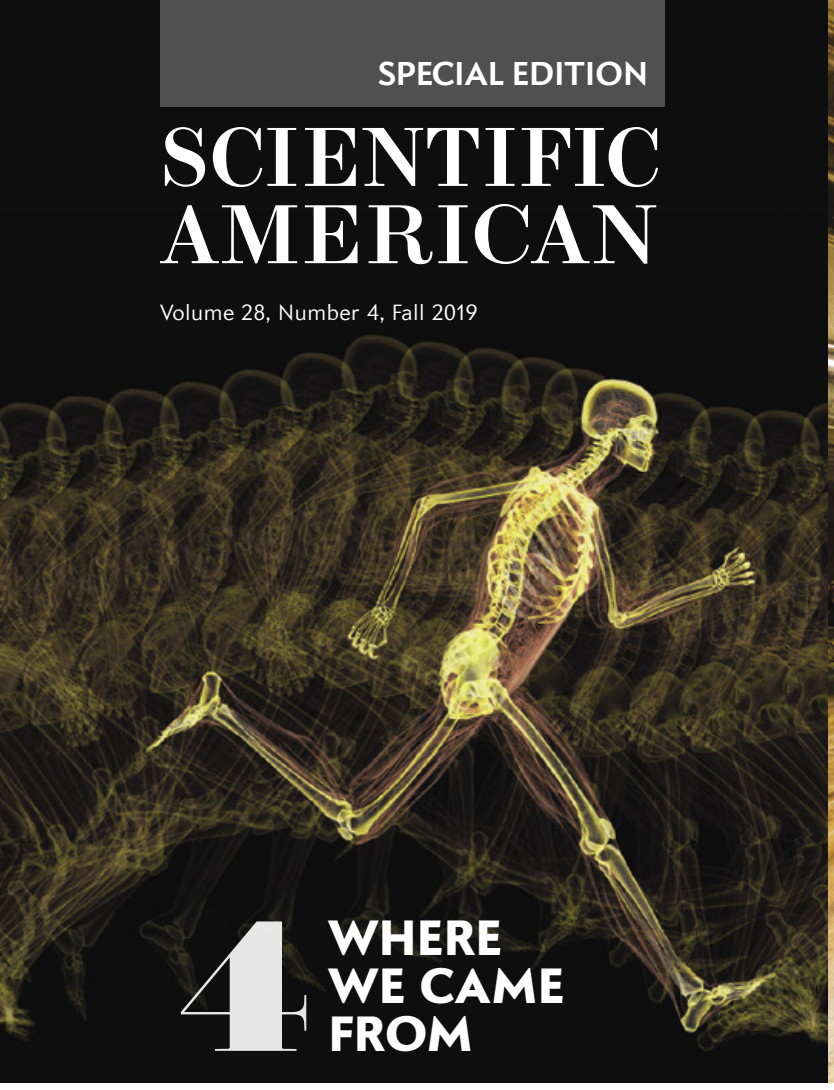

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LAST HOMININ STANDING

Why did *Homo sapiens* alone survive to the modern era?

By Kate Wong

Illustration by Yuko Shimizu

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AT THE DAWNING OF *HOMO SAPIENS,* OUR ANCESTORS were born into a world we would find utterly surreal. It's not so much that the climate and sea levels or the plants and the animals were different, although of course they were—it's that there were other kinds of humans alive at the same time. For most of *H. sapiens*' existence, in fact, multiple human species walked the earth. In Africa, where our species got its start, large-brained *Homo heidelbergensis* and small-brained *Homo naledi* also roamed. In Asia, there was *Homo erectus,* a mysterious group dubbed the Denisovans and, later, *Homo floresiensis*—a hobbitlike creature, tiny but for its large feet. The stocky, heavy-browed Neandertals, for their part, ruled Europe and western Asia. And there were probably even more forms, as yet undiscovered.

IN BRIEF

Until recently, the dominant model of human origins held that *Homo sapiens* arose in a single region of Africa and replaced archaic human species throughout the Old World without interbreeding with them. **New findings** from archaeology, paleontology and genetics are rewriting that story. **The latest research** suggests that *H. sapiens* emerged from groups located across Africa and that interbreeding with other human species contributed to our success.

By around 40,000 years ago, based on current evidence, *H. sapiens* found itself all alone, the only remaining member of what was once an incredibly diverse family of bipedal primates, together known as hominins. (In this article, the terms "human" and "hominin" both refer to *H. sapiens* and its extinct relatives.) How did our kind come to be the last human standing?

Until a few years ago, scientists favored a simple explanation: *H. sapiens* arose relatively recently, in more or less its current form, in a single region of Africa and spread out from there into the rest of the Old World, supplanting the Neandertals and other archaic human species it encountered along the way. There was no appreciable interspecies fraternizing, just wholesale replacement of the old guards by the clever newcomer, whose ascendancy seemed inevitable.

Yet mounting evidence from fossil and archaeological discoveries, as well as DNA analyses, has experts increasingly rethinking that scenario. It now looks as though *H. sapiens* originated far earlier than previously thought, possibly in locations across Africa instead of a single region, and that some of its distinguishing traits—including aspects of the brain—evolved piecemeal. Moreover, it has become abundantly clear that *H. sapiens* actually did mingle with the other human species it encountered and that interbreeding with them may have been a crucial factor in our success. Together these findings paint a far more complex picture of our origins than many researchers had envisioned—one that privileges the role of dumb luck over destiny in the success of our kind.

THEORY UNDER THREAT

DEBATE ABOUT THE ORIGIN of our species has traditionally focused on two competing models. On one side was the Recent African Origin hypothesis, championed by paleoanthropologist Christopher Stringer and others, which argues that *H. sapiens* arose in either eastern or southern Africa within the past 200,000 years and, because of its inherent superiority, subsequently replaced archaic hominin species around the globe without interbreeding with them to any significant degree. On the other was the Multiregional Evolution model, formulated by paleoanthropologists Milford Wolpoff, Xinzhi Wu and Alan Thorne, which holds that modern *H. sapiens* evolved from Neandertals and other archaic human populations throughout the Old World, which were connected through migration and mating. In this view, *H. sapiens* has far deeper roots, reaching back nearly two million years.

By the early 2000s the Recent African Origin model had a wealth of evidence in its favor. Analyses of the DNA of living people indicated that our species origi-

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nated no more than 200,000 years ago. The earliest known fossils attributed to our species came from two sites in Ethiopia, Omo and Herto, dated to around 195,000 and 160,000 years ago, respectively. And sequences of mitochondrial DNA (the tiny loop of genetic material found in the cell's power plants, which is different from the DNA contained in the cell's nucleus) recovered from Neandertal fossils were distinct from the mitochondrial DNA of people today—exactly as one would expect if *H. sapiens* replaced archaic human species without mating with them.

Not all of the evidence fit with this tidy story, however. Many archaeologists think that the start of a cultural phase known as the Middle Stone Age (MSA) heralded the emergence of people who were beginning to think like us. Prior to this technological shift, archaic human species throughout the Old World made pretty much the same kinds of stone tools fashioned in the so-called Acheulean style. Acheulean technology centered on the production of hefty hand axes that were made by taking a chunk of stone and chipping away at it until it had the desired shape.

With the onset of the MSA, our ancestors adopted a new approach to toolmaking, inverting the knapping process to focus on the small, sharp flakes they detached from the core—a more efficient use of raw material that required sophisticated planning. And they began attaching these sharp flakes to handles to create spears and other projectile weapons. Moreover, some people who made MSA tools also made items associated with symbolic behavior, including shell beads for jewelry and pigment for painting. A reliance on symbolic behavior, including language, is thought to be one of the hallmarks of the modern mind.

The problem was that the earliest dates for the MSA were more than 250,000 years ago—far older than those for the earliest *H. sapiens* fossils at less than 200,000 years ago. Did another human species invent the MSA, or did *H. sapiens* actually evolve far earlier than the fossils seemed to indicate?

In 2010 another wrinkle emerged. Geneticists announced that they had recovered nuclear DNA from Neandertal fossils and sequenced it. Nuclear DNA makes up the bulk of our genetic material. Comparison of the Neandertal nuclear DNA with that of living people revealed that non-African people today carry DNA from Neandertals, showing that *H. sapiens* and Neandertals did interbreed after all, at least on occasion.

Subsequent ancient genome studies confirmed that Neandertals contributed to the modern human gene pool, as did other archaic humans. Further, contrary to the notion that *H. sapiens* originated within the past 200,000 years, the ancient DNA suggested that Neandertals and *H. sapiens* diverged from their common ancestor considerably earlier than that, perhaps upward of half a million years ago. If so, *H. sapiens* might have originated more than twice as long ago as the fossil record indicated.

ANCIENT ROOTS

RECENT DISCOVERIES at a site called Jebel Irhoud in Morocco have helped bring the fossil, cultural and genetic evidence into better alignment—and bolstered a new view of our origins. When barite miners first discovered fossils at the site back in 1961, anthropologists thought the bones were around 40,000 years old and belonged to Neandertals. But over the years continued excavations and analyses led researchers to revise that assessment. In June 2017 paleoanthropologist Jean-Jacques Hublin of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and his colleagues announced that they had recovered additional fossils from the site, along with MSA tools. Using two dating techniques, they estimated the remains to be roughly 315,000 years old. The researchers had found the oldest traces of *H. sapiens* to date, as well as the oldest traces of MSA culture—pushing back the fossil evidence of our species by more than 100,000 years and linking it to the earliest known appearance of the MSA.

Not everyone agrees that the Jebel Irhoud fossils belong to *H. sapiens*. Some experts think they may instead come from a close relative. But if Hublin and his collaborators are right about the identity of the bones, the constellation of skull traits that distinguish *H. sapiens* from other human species did not all emerge in lockstep at the inception of our kind, as supporters of the Recent African Origin theory had supposed. The fossils resemble modern humans in having a small face, for example. But the braincase is elongated like those of archaic human species rather than rounded like our own dome. This shape difference reflects differences in brain organization: compared with fully modern humans, the Jebel Irhoud individuals had smaller parietal lobes, which process sensory input, and a smaller cerebellum, which is involved in language and social cognition, among other functions.

Neither do the archaeological remains at Jebel Irhoud exhibit the full complement of MSA features. The people there made MSA stone tools for hunting and butchering gazelles that roamed the grasslands that once carpeted this now desert landscape. And they built fires, probably to cook their food and warm themselves against the chill of night. But they did not leave behind any traces of symbolic expression.

In fact, on the whole, they are not especially more sophisticated than the Neandertals or *H. heidelbergensis*. If you could journey back in time to our species' debut, you wouldn't necessarily pick it to win the evolutionary sweepstakes. Although early *H. sapiens* had some innovations, "there weren't any big changes at 300,000 years ago that indicate they were destined to be successful," observes archaeologist Michael Petraglia of the Max Planck Institute for

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the Science of Human History in Jena, Germany. "In the beginning with *sapiens,*" Petraglia says, "it looks like anyone's game."

GARDENS OF EDEN

THE TOTAL *H. SAPIENS* PACKAGE, many researchers agree, did not coalesce until sometime between 100,000 and 40,000 years ago. So what happened in the intervening 200,000 years or more to transform our species from run-of-the-mill hominin to world-conquering force of nature? Scientists are increasingly thinking about how the size and structure of the early *H. sapiens* population might have factored into the metamorphosis. In a paper published online in 2018 in *Trends in Ecology & Evolution,* archaeologist Eleanor Scerri of the University of Oxford and a large interdisciplinary group of co-authors, including Stringer, make the case for what they call the African Multiregionalism model of *H. sapiens* evolution. The scientists note that the earliest putative members of our species—namely, the Jebel Irhoud fossils from Morocco, the Herto and Omo Kibish fossils from Ethiopia, and a partial skull from Florisbad, South Africa—all look far more different from one another than people today do. So much so that some researchers have argued that they belong to different species or subspecies. "But maybe early *H. sapiens* was just ridiculously diverse," Scerri offers. And maybe looking for a single point of origin for our species, as many researchers have been doing, is "a wild goose chase," she says.

> We may actually owe our extinct relatives a substantial debt of gratitude for our success.

When Scerri and her colleagues examined the latest data from fossils, DNA and archaeology, the emergence of *H. sapiens* began to look less like a single origin story and more like a pan-African phenomenon. Rather than evolving as a small population in a particular region of Africa, they propose, our species emerged from a large population that was subdivided into smaller groups distributed across the vast African continent that were often semi-isolated for thousands of years at a time by distance and by ecological barriers such as deserts. Those bouts of solitude allowed each group to develop its own biological and technological adaptations to its own niche, be it an arid woodland or a savanna grassland, a tropical rain forest or a marine coast. Every so often, however, the groups came into contact with one another, allowing for both genetic and cultural exchange that fed the evolution of our lineage.

Shifting climate could have fueled the fracturing and rejoining of the subpopulations. For instance, paleoenvironmental data have shown that every 100,000 years or so, Africa enters into a humid phase that transforms the forbidding Sahara Desert into a lush expanse of vegetation and lakes. These green Sahara episodes, as they are known, would have allowed populations formerly isolated by the harsh desert to link up. When the Sahara dried out again, populations would be sequestered anew and able to undergo their own evolutionary experiments for another stretch of time until the next greening.

A population subdivided into groups that each adapted to their own ecological niche, even as occasional migration between groups kept them connected, would explain not only the mosaic evolution of *H. sapiens*' distinctive anatomy but also the patchwork pattern of the MSA, Scerri and her co-authors argue. Unlike Acheulean tools, which look mostly the same everywhere they turn up throughout the Old World, MSA tools exhibit considerable regional variation. Sites spanning the time between 130,000 and 60,000 years ago in North Africa, for example, contain tool types not found at sites in South Africa from the same interval, including stone implements bearing distinctive stems that may have served as attachment points for handles. Likewise, South African sites contain slender, leaf-shaped tools made of stone that was heated to improve its fracture mechanics—no such implements appear in the North African record. Complex technology and symbolism become more common over time across the continent, but each group acts its own way, tailoring its culture to its specific niche and customs.

H. sapiens was not the only hominin evolving bigger brains and sophisticated behaviors, however. Hublin notes that human fossils from China dating to between 300,000 and 50,000 years ago, which he suspects belong to Denisovans, exhibit increased brain size. And Neandertals invented complex tools, as well as their own forms of symbolic expression and social connectedness, over the course of their long reign. But such behaviors do not appear to have become as highly developed or as integral to their way of life as they eventually did in ours, observes archaeologist John Shea of Stony Brook University, who thinks that advanced language skills allowed *H. sapiens* to prevail.

"All these groups are evolving in the same direction," Hublin says. "But our species crosses a threshold before the others in terms of cognitive ability, social complexity and reproductive success." And when it does—around 50,000 years ago, in Hublin's estimation—"the boiling milk escapes the saucepan." Forged and honed in Africa, *H. sapiens* could now enter virtually any environment on the earth and thrive. It was unstoppable.

CLOSE ENCOUNTERS

HUNDREDS OF THOUSANDS of years of splitting up from and reuniting with members of our own species

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might have given *H. sapiens* an edge over other members of the human family. But it was not the only factor in our rise to world domination. We may actually owe our extinct relatives a substantial debt of gratitude for their contributions to our success. The archaic human species that *H. sapiens* met as it migrated within Africa and beyond its borders were not merely competitors—they were also mates. The proof lies in the DNA of people today: Neandertal DNA makes up some 2 percent of the genomes of Eurasians; Denisovan DNA composes up to 5 percent of the DNA of Melanesians. And a recent study by Arun Durvasula and Sriram Sankararaman, both at the University of California, Los Angeles, found that nearly 8 percent of the genetic ancestry of the West African Yoruba population traces back to an unknown archaic species. Other genetic evidence from contemporary populations suggests that *H. sapiens* also interbred with unknown extinct hominins in South and East Asia.

Some of the DNA that *H. sapiens* picked up from archaic hominins may have helped our species adapt to the novel habitats it entered on its march across the globe. When geneticist Joshua Akey of Princeton University and his colleagues studied the Neandertal sequences in modern human populations, they found 15 that occur at high frequencies, a sign that they had beneficial consequences. These high-frequency sequences cluster into two groups. About half of them influence immunity. "As modern humans dispersed into new environments, they were exposed to new pathogens and viruses," Akey says. Through interbreeding, "they could have picked up adaptations from Neandertals that were better able to fight off those new pathogens," he explains.

The other half of the Neandertal sequences that Akey's team found at high frequency in modern human populations are related to skin, including genes that influence pigmentation levels. Researchers have previously theorized that *H. sapiens* individuals from Africa, who presumably had darker skin to protect against harmful ultraviolet radiation from the sun, would have had to evolve lighter skin as they entered northern latitudes to get enough vitamin D, which the body acquires mainly through sun exposure. Skin genes from Neandertals may have aided our predecessors in doing exactly that.

Neandertals are not the only archaic humans who gave us useful genes. For example, modern-day Tibetans have the Denisovans to thank for a gene variant that helps them cope with the low-oxygen environment of the high-altitude Tibetan plateau. And contemporary African populations have inherited from an unknown archaic ancestor a variant of a gene that may help fend off bad bacteria inside the mouth.

Interbreeding with archaic humans who had millennia to evolve adaptations to local conditions may well have allowed invading *H. sapiens* to adjust to novel environments faster than if it had to wait for favorable mutations to crop up in its own gene pool. But it's not all upside. Some of the genes we obtained from Neandertals are associated with depression and other diseases. Perhaps these genes were advantageous in the past and only began causing trouble in the context of modern ways of life. Or maybe, Akey suggests, the risk of developing these diseases was a tolerable price to pay for the benefits these genes conferred.

Archaic humans may have contributed more than DNA to our species. Researchers have argued that contact between divergent human groups probably led to cultural exchange and may have even spurred innovation. For example, the arrival of *H. sapiens* in western Europe, where the Neandertals long resided, coincided with an uncharacteristic burst of technological and artistic creativity in both groups. Previously some experts suggested that Neandertals were simply aping the inventive newcomers. But maybe it was the interaction between the two groups that ignited the cultural explosion on both sides.

In a sense, the fact that *H. sapiens* mixed with other human lineages should not come as a surprise. "We know from many animals that hybridization has played an important role in evolution," observes biological anthropologist Rebecca Rogers Ackermann of the University of Cape Town in South Africa. "In some cases, it can create populations, and even new species, that are better adapted to new or changing environments than their parents were because of novel traits or novel combinations of traits." Human ancestors show a similar pattern: the combination of different lineages resulted in the adaptable, variable species we are today. "*Homo sapiens* is the product of a complex interplay of lineages," Ackermann asserts, and it has flourished precisely because of the variation that arose from this interplay. "Without it," she says, "we simply wouldn't be as successful."

How often such mingling occurred and the extent to which it helped drive evolution in *H. sapiens* and other hominins remain to be determined. But it may be that the particular environmental and demographic circumstances in which our species found itself in Africa and abroad led to more opportunities for genetic and cultural exchange with other groups than our fellow hominins experienced. We got lucky—and are no less marvelous for it. SA

Kate Wong is a senior editor for evolution and ecology at *Scientific American.*

MORE TO EXPLORE

The Hybrid Origin of "Modern" Humans. Rebecca Rogers Ackermann et al. in *Evolutionary Biology,* Vol. 43, No. 1, pages 1–11; March 2016.

Did Our Species Evolve in Subdivided Populations across Africa, and Why Does It Matter? Eleanor M. L. Scerri et al. in *Trends in Ecology & Evolution.* Published online July 11, 2018.

FROM OUR ARCHIVES

Human Hybrids. Michael F. Hammer; May 2013.

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Climate Shocks

Swings between wet and dry landscapes pushed some of our ancestors toward modern traits—and killed off others

By Peter B. deMenocal

AMID THE DESERTS of East Africa, Lake Turkana has swelled and disappeared dozens of times while our ancestors were evolving here.

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SCRAMBLING UP THE STEEP BANK OF A SMALL WADI, or gully, near the western shore of Lake Turkana in northern Kenya, I stop on a little knoll that offers a view across the vast, mostly barren desert landscape. The glittering, jade-blue lake contrasts in every way with the red-brown landscape around it. This long, narrow desert sea, nestled within Africa's Great Rift Valley, owes its existence to the Omo River, whose winding flow delivers runoff that comes from summer monsoon rains in the Ethiopian highlands, hundreds of miles north.

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The heat here has to be respected. By noon it feels like a blast furnace. The sun beats down, and the hot, stony ground fires it back upward. Scanning the dusty horizon, with the lake winking in the distance, I find it hard to imagine this place as anything but a desert.

Yet evidence for much wetter times is everywhere. Indeed, the little hillock under my boots is a thick chunk of ancient lake sediments that date back 3.6 million years, when a much larger and deeper Lake Turkana filled this basin to the brim. The glassy remains of fossil lake algae make up white, sandy layers, and large fish fossils are common. At times in the past, this rocky desert was carpeted with grasslands and trees and lakes.

Such climate changes may have played a big role in shaping human evolution, a growing number of scientists believe. The Lake Turkana region, together with other sites in East and South Africa, possesses most of the fossil record of early human origins and our evolutionary journey since our lineage split from African apes more than seven million years ago.

Remarkably, major shifts in African climate coincide with two moments on that ancestral path, roughly a million years apart, that mark significant changes in our family tree. The first evolutionary shake-up happened between 2.9 million and 2.4 million years ago. The famous ancestral lineage of "Lucy" and her ilk (*Australopithecus afarensis*) became extinct, and two other, quite distinctive groups appeared. One of them had the hints of some modern-looking traits, including larger brains. Their owners were the very first members of our own genus, *Homo*. Crude stone tools appeared near these fossils. The other group besides *Homo* that emerged at this time looked different: a stoutly built, heavy-jawed and ultimately unsuccessful lineage known collectively as *Paranthropus*.

The second shake-up occurred between 1.9 million and 1.6 million years ago. An even larger-brained and more carnivorous species, *Homo erectus* (called *Homo ergaster* by some scientists), appeared on the scene. Its taller, more lithe skeleton was nearly indistinguishable from that of modern humans. This species was also the first to leave Africa to populate Southeast Asia and Europe. Stone-tool technology also got a major upgrade: the first hand axes showed up, with large blades carefully shaped on two sides.

Why were these evolutionary milestones, harbingers of modern humanity, so clustered in time? A number of scientists now think two episodes of climate change may have been the cause. These two ecological jolts, coming after long periods of extremely gradual change, moved the cradle of humanity toward increasingly dry and open grasslands. While these broader shifts were happening, the climate whipsawed rapidly between wet and dry periods, so to thrive, our ancestors had to adapt to rapidly changing landscapes.

The evidence comes from an array of data that tell us how and why African climate and vegetation changed during these big human evolutionary moments. Scientists are now able to extract and analyze molecular remnants of ancient African vegetation from layers of sediments such as the ones I stood on. Chemical analyses of our ancestors' teeth reveal what they ate as the landscape changed. The creatures that adapted to these shifts—those that showed flexibility in what they ate and where they lived—appear to be the ones that prospered. This emphasis on flexibility in the face of new environmental challenges seems to be a trait that carries forward in the human lineage. Other forebears, who did not appear to change with the times, died out. Rick Potts, a paleoanthropologist at the Smithsonian Institution, calls the role of flexibility in making us what we are "variability selection."

LIFE SHAPED BY CLIMATE

THEORIES LINKING CLIMATE CHANGE and evolution go back to Charles Darwin. His premise was that large-scale shifts in climate can shake up the kinds of food, shelter and other resources available in a given region. The disappearance of a favorite food or the replacement of a long wet season with a longer dry one create pressures that lead, eventually, to adaptation, extinction or evolution into different species. The environment, set by climate, will favor creatures with genes for certain advantageous traits, such as larger brains. Over time, those creatures and the genes they carry will come to dominate because more of them will survive. In *On the Origin of Species,* Darwin noted that seasons of extreme cold or drought were effective checks on species numbers.

This process of change is not always subtle or gentle. Each of the "big five" mass extinctions in the fossil record of life on earth during the past 540 million years was accompanied by an environmental disruption. During each of these events, between 50 and 90 percent of all species perished, but this was followed by bursts of new, very different species. These episodes define the major chapters in the history book of life, when new biotic worlds emerged and flourished. We mammals owe a debt of gratitude to the Manhattan-size meteorite that struck the Yucatán Peninsula in what is now Mexico about 66 million years ago. It killed off the dinosaurs (and numerous other less charismatic species), ushering in the rapid radiation and diversification of mammals.

One group of those mammals led, after many more branchings and a lot of time, to us. For these hominins (modern humans and our extinct relatives), scientists have tried out several ideas about the way the environment shaped evolution. The "savanna hypothesis" was one. In its earliest incarnation, scientists proposed that our early human ancestors, with burgeoning bipedality, large brains and toolmaking, were better suited to rapidly expanding savanna grasslands, where competition for resources was fiercer, and they left our apelike forebears behind in receding forests.

IN BRIEF

Changes in climate are emerging as elements that shaped human evolution over millions of years, as scientists learn that such alteration coincided with the extinction of some of our ancestors and the success of others.

Evidence from ancient soils in East Africa, deep-sea sediments and fossil teeth from our forerunners combines to reveal rapid swings between wet and dry environments, as well as two distinct periods when grasslands replaced more wooded areas.

The emergence of our own genus, *Homo,* our varied diet, advances in stone-tool technology and the very human trait of adaptability in the face of ongoing change may be tied to these episodes, according to one theory.

PRECEDING PAGES: YASUYOSHI CHIBA *Getty Images*

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STONE AGE EATING: A distant ancestor, *Paranthropus boisei* (*1*), lived in open plains and mostly ate grasses or related foods, as indicated by chemical analysis of fossil teeth. But *Homo erectus*, sometimes called *Homo ergaster* (*2*), a member of our own genus that lived in the same landscape, had a more varied diet, and adaptability may have helped its evolutionary success.

This dated view, which still shows up in some textbooks, is incorrect. There was no one-time habitat switch from forests to grasslands but rather a rapid succession of wet-dry cycles that moved, in distinct steps, toward drier conditions. Also, we did not acquire human traits in one single moment but rather in a series of concentrated bursts just when the environment was shifting.

WET AND DRY CYCLES

EVIDENCE FOR THESE BURSTS of landscape change and evolution comes not just from land but from the sea. African ground sediments are often hard to analyze because of erosion and other geologic disturbances. In the deep oceans, however, they remain undisturbed. By drilling into the seafloor near the African coasts, geologists like myself have been able to penetrate a multimillion-year time capsule, recovering long cores of sediments that preserve complete records of past African environments. To get these cores, we need a special ship. That is why a team of 27 scientists and I spent two months in the fall of 1987 on the 470-foot drilling vessel *JOIDES Resolution*.

"Core on deck!" the driller over the PA system would squawk in his Texan twang. We scientists groaned, donned our hard hats, and marched out of the ship's cool, comfortable laboratories into the blinding Arabian sun to carry yet another 30-foot segment of deep-sea sediment core inside for analysis. The *Resolution* is an internationally funded research ship designed to explore and drill the ocean bottom and recover the earth's history recorded there. We were drilling through layers of deep-sea sediment in the Arabian Sea in a mile and a half of water, taking cores from nearly half a mile into the sea bottom. Since the divergence of great ape and human lineages several million years ago, the ocean bottom here had accumulated nearly 1,000 feet of deep-sea mud in the dark, peaceful abyss, at a rate of about one and a half inches every 1,000 years.

The sediments here consist of mixtures of fine-white calcium carbonate fossil shells from ancient ocean plankton and darker, silty grains of dirt blown from areas of Africa and Arabia by windy monsoons. When the mix looks darker and gritty, it indicates drier, dustier times. When it looks lighter, that reflects wetter, more humid conditions.

Laying the split sediment core on a table inside the ship's spacious research labs, we could see that the alternating light and dark layers repeated every three feet, more or less, which meant they changed about every 23,000 years. It was clear that African climate history had been one of continuous swings between wetter and drier times. That was nothing like a single, sharp shift to a savanna.

These swings reflected the known sensitivity of African and Asian monsoonal climates to the earth's orbital wobble, which occurs as a regular 23,000-year cycle. The wobble changes the amount of sunlight hitting our planet in a given season. For North Africa and South Asia, more or less heat during the summer increased or decreased monsoon rainfall, making these regions either much wetter or drier as our planet wobbled back and forth.

Just how wet things got is recorded in magnificent rock art drawn between 10,000 and 5,000 years ago by humans during the most recent wet period in North Africa. Art found across the Sahara depicts lush landscapes filled with elephants, hippopotamuses, giraffes, crocodiles and bands of hunters chasing gazelles. The Sahara was covered with grass and trees; lake basins, now overrun by sand dunes, were filled to the brim with water. A swollen Nile River rushed into the eastern Mediterranean, and black, organic-rich sediments called sapropels accumulated on the Mediterranean seafloor. They alternated with whiter layers laid down during dry periods, a bar-code message telling of African climate cycles reaching deep into the past, just like the changing dust layers recovered from the Arabian Sea.

RECONSTRUCTION AND PHOTOGRAPH © 2014 JOHN GURCHE (1); FROM *SHAPING HUMANITY*, BY JOHN GURCHE; YALE UNIVERSITY PRESS, 2013 (2)

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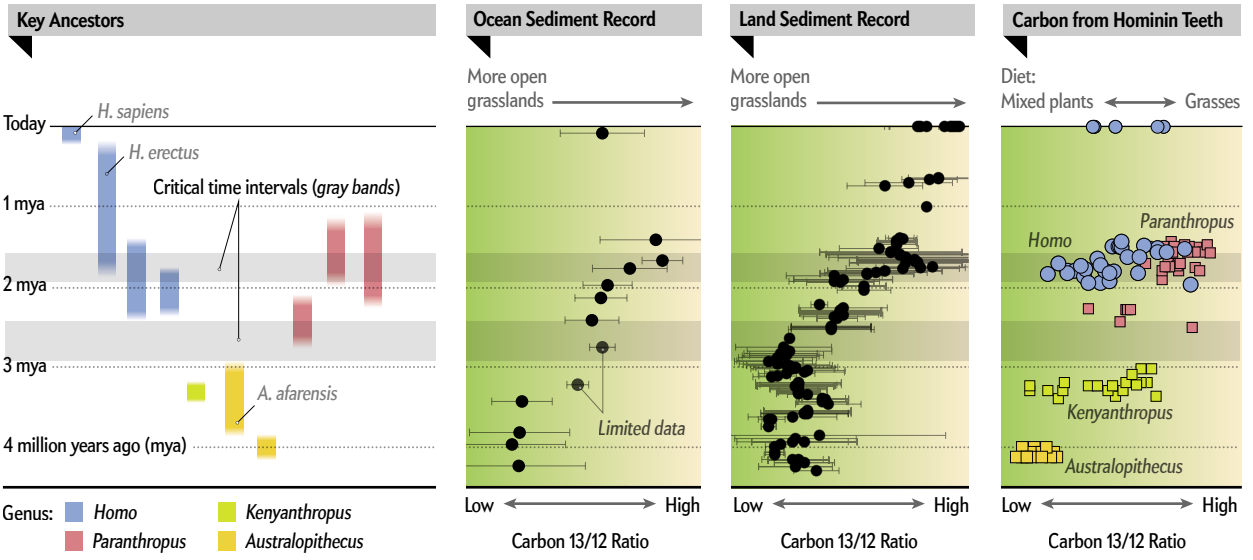
A Climate for Change

Two moments in our evolutionary history show a tantalizing connection between climate swings and the life and death of key members of our family tree. Starting just after three million years ago, the species *Australopithecus afarensis* vanished, and the groups *Paranthropus* and *Homo* (our own genus) appeared. During this period, changes in carbon isotope ratios from land and ocean sediments show that dry grasslands rapidly expanded and wetter woodlands shrank. Starting after two million years ago, *Homo erectus,* one of our direct ancestors, appeared and migrated out of Africa. Again, the carbon evidence shows grasslands got another boost. Yet carbon in the teeth from *H. erectus* indicates the consumption of a mixed diet and an ability to find food from a variety of sources even as grasslands enlarged. *Paranthropus* teeth, however, showed the group (like an earlier extinct forebear, *Kenyanthropus*) was restricted to eating from grassy surroundings.



THE LAST OF LUCY

SUPERIMPOSED ON THESE orbital wet-dry cycles were larger steps toward dry and open grasslands. Small patches of grasslands first expanded in East Africa nearly eight million years ago. But vast grassy plains such as the Serengeti were only established permanently after three million years ago. Just about this time, our evolutionary history was given a jolt as well.

We lost Lucy. Her extremely successful species, *A. afarensis,* had survived in East Africa for 900,000 years, starting at about 3.9 million years ago. But just under three million years ago, Lucy's kind disappeared from the fossil record.

Next the *Paranthropus* group appeared, followed 2.6 million years ago by the first signs of stone choppers and scrapers and then in a few hundred thousand years by early *Homo* fossils.

We know these changes in our family tree and in technological invention happened during a shift in overall climate because of some clever scientific detective work, tracing the fingerprints left by some plants that flourished in wetter environments and others that thrived in drier times.

Savannas are open tropical ecosystems composed of grasses and sedges, sometimes spotted with clusters of woody trees. Savanna grasses do very well in hot, dry regions because, to take up carbon from the atmosphere, they use a specific photosynthetic pathway called C4. This set of reactions is miserly with carbon and water, an adaptation to life in dry and low-CO_2 environments. Woody vegetation such as trees finds homes in wetter ecosystems because it uses another photosynthetic pathway called C3, which requires much more water.

Thure E. Cerling and his colleagues at the University of Utah developed a way to reconstruct the vegetation history of ancient landscapes. Some years ago researchers discovered that C4 grasses have a greater abundance of the heavier but rarer carbon 13 isotope relative to the lighter, more abundant carbon 12 isotope. But C3 shrubs and woody plants have a lower carbon 13/12 ratio. The scientists discovered that they could take samples of soil or nodules of rock from a given landscape, analyze the carbon ratios, and use them to accurately estimate the percentage of C4 grasses versus C3 woody plants that were once in that area.

When they looked at the East African sediment from sites that had yielded fossil hominins, the researchers learned that East African landscapes were predominantly C3 forest and shrublands before eight million years ago. After that, the proportion of C4 grasslands increased gradually. Then a relatively large and fast shift occurred between three million and two million years ago.

During this shift, grasslands expanded rapidly across present-day Kenya, Ethiopia and Tanzania. The spread was accompanied by a rise in the proportion of grazing mammals, shown by their abundant fossils. As time ticked forward, closer to two million years ago, African antelopes—their horns, whose different shapes indicate different species, are well preserved—seem to have undergone extensive speciation, extinction and adaptation, rather like our hominin forebears.

SOURCE: PETER B. DEMENOCAL

Graphic by Jen Christiansen

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Bovids, the family to which these even-toed ungulates belong, represent roughly one third of all African fossils. Thus, they provide a much larger data set than do the far scarcer hominins. Paleontologist Elisabeth Vrba of Yale University conducted an all-Africa analysis of bovid evolution spanning the past six million years. Her study identified specific times when rates of bovid speciation and extinction were well above normal background levels. The two largest of these events occurred near 2.8 million and 1.8 million years ago, coinciding with the periods of grassland growth that geologists observe, although recent work by René Bobe, now at George Washington University, and Anna K. Behrensmeyer of the Smithsonian Institution suggests these events may be more muted. The anatomy of these fossils hints that some of them were taking advantage of the landscape change. For example, many new grazing bovid species appeared with specialized molars for chewing the abrasive, grassy diet.

DIETS AND LANDSCAPES

AS WAS THE CASE FOR BOVIDS, this vegetation change most likely had a profound effect on our own ancestors because we do not just live in an environment—we eat it. Paleo diet research turns out to be quite useful for understanding how hominins were affected by changing landscapes. Just as isotopes in soils can be used to infer the relative abundance of grasslands in an ancient landscape, scientists have recently started to analyze the isotopic composition in our forerunners' fossil teeth. The carbon isotope analysis of a tooth from a modern American would sit squarely on the C4-grass side of the scale because much of what we consume—meat from cows, soft drinks, snacks, sweets—derives from corn, a C4 grass.

Prehistoric diet changes seem to be part of that second big evolutionary moment in our history, nearly two million years ago, when *Homo* fossils that looked more modern first appeared. Cerling and his many colleagues have been examining the teeth of Turkana Basin fossils. Some years ago they published a remarkable study that showed a dietary split between early members of our own genus, *Homo,* and members of the heavy-jawed *Paranthropus* group, at just under that two-million-year mark. One species, *Paranthropus boisei,* has sometimes been called Nutcracker Man because of its impressively large molars and massive jawbones. The carbon isotope tooth data from this species indicate it indeed ate a narrow, mostly C4-based diet. Fine microscopic scratches on the teeth, however, suggest it was not cracking nuts at all but rather eating soft C4 grasses and sedges.

The big surprise was for *Homo*. These early teeth recorded a diet that bucked the landscape trend toward greater C4 grass cover. The tooth isotopic data for early *Homo* indicate a strikingly mixed, roughly 65–35 diet of C3- and C4-based foods. It shows that *Homo* sought diverse foods from a landscape that was becoming increasingly uniform. Early *Homo* had a varied, flexible diet and passed its genes to subsequent lineages, eventually leading to us. *Paranthropus,* in contrast, lived in a narrow C4 dietary niche and eventually became extinct.

It is tempting to speculate that the more complex stone tools that appeared with this group of *Homo*—hand axes, cleavers and the like, tools that required more effort to fashion and could be put to multiple uses—were better suited to help their owners exploit varying food sources. We are still not at all sure what these organisms were eating, but we do know which dietary adaptations were ultimately successful.

FILLING IN THE CLIMATE GAPS

THIS C3/C4 STORY, though intriguing, has some holes in it: in particular, gaps of several thousands of years in land sediment sequences. But again, the ocean sediments and their more complete records can help fill in the blanks. A very promising technique for continuously tracking vegetation changes has emerged in the past decade. All terrestrial plants have waxy leaf coatings that protect them from injury and dehydration. When plants die or become abraded, the waxy coatings are carried by the winds, along with mineral dust and other particles. These coatings are made out of tough little molecules, long carbon-based chains known as lipids. They are resistant to degradation and possess the carbon isotopic signature from their host plant type, C3 or C4. Once chemically isolated from sediments, these plant wax lipids can be measured and their carbon signature determined as C3 or C4. The relative abundance of a particular type lets us estimate the amounts of grass versus trees and scrubs on ancient landscapes.

Sarah J. Feakins, now at the University of Southern California, and her colleagues applied this technique to reconstruct hominin environments. Analyzing sediments from a drilling site in the Gulf of Aden, she confirmed that East African grasslands expanded between three million and two million years ago, perhaps by as much as 50 percent. Feakins also found that these plant wax biomarkers varied within the dust layers that marked the short-term swings driven by orbital cycles and monsoons. The grasses and woodlands shifted back and forth on this shorter scale, and many of these swings were nearly as large as the long-term shift to more open, grassy landscapes. At the famous fossil site Olduvai Gorge in Tanzania, where hominins lived 1.9 million years ago, scientists Clayton R. Magill and Katherine H. Freeman, both then at Pennsylvania State University, found similar biomarker shifts.

We are closing in on a clearer picture of the how and why of human origins. Gone is the old image of our ancestors emerging from some ancient dark forest to assert dominion over the grassy plains. In its place is new evidence for a series of rapid climate cycles and two large shifts that established the African savanna we know today. Some evidence indicates that our most successful forebears had the flexibility to adapt to these changes. Researchers are already trying to firm up this connection between climate and these evolutionary events with more detailed investigations. Still, it appears as if an answer to the age-old question "How did I get here?" is no longer beyond our reach. SA

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MORE TO EXPLORE

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THE NEW ORIGINS OF TECHN

ARCHAEOLOGISTS at a site in northwestern Kenya called Lomekwi 3 have unearthed the oldest stone tools in the world.

Photographs by Andrew Renneisen

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ANCIENT STONE TOOLS FROM KENYA SHATTER THE CLASSIC STORY OF WHEN AND HOW HUMANS BECAME INNOVATORS

By Kate Wong

OLOGY

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The desert badlands on the northwestern shores of Kenya's Lake Turkana offer little to the people who live there. Drinking water is elusive, and most of the wild animals have declined to near oblivion. The Turkana scrape by as pastoralists, herding goats, sheep, cattle, donkeys and the occasional camel in the hot, arid countryside. It is a hard life. But millions of years ago the area brimmed with freshwater, plants and animals. It must have been paradise for the human ancestors who settled here.

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Sonia Harmand has come to this region to study the legacy these ancestors left in stone. Harmand is an archaeologist at Stony Brook University. She has an intense gaze and a commanding presence. On a hazy July morning Harmand sits at a small, wood folding table, scrutinizing a piece of rock. It is brownish-gray, about the size of her pinkie fingernail, and utterly unremarkable to the untrained eye. But it is exactly what she has been looking for.

Nearby 15 workers from Kenya, France, the U.S. and England are digging their way into the side of a low hill. They tap hammers against chisels to chip away at the buff-colored sediments, searching for any bits of rock that could signal ancient human activity. At the top of the hill, the workers' water bottles hang like Christmas ornaments on the thorny branches of an acacia tree; the early breeze will keep their contents cool a little longer before the heat of the day sets in. By afternoon the air temperature will top 100 degrees Fahrenheit, and the excavation floor, windless and sun-cooked, will live up to its nickname: the Oven.

In 2015 Harmand and her husband, Jason Lewis, a paleoanthropologist at Stony Brook, announced that their team had discovered 3.3-million-year-old stone tools at this site, which is called Lomekwi 3. They were the oldest stone tools ever found by far—so old that they challenged a cherished theory of human evolution. The scientists want to learn who made the tools and why. But they also have a more immediate task: unearthing more evidence that the tools are, in fact, as old as they appear.

The fragment in Harmand's hand is the first evidence of ancient stone-tool production the researchers have recovered since they got here. It is a piece of debris produced by knapping—the act of striking one rock against another to produce a sharp-edged flake. Small and light, the fragment implies that the site has not been disturbed by flowing water in the millions of years since. That fact, in turn, supports the argument that the Lomekwi 3 tools come from this ancient sedimentary layer and not a younger one. Now that the excavators have hit the artifact-bearing level of the site, they must proceed with care. "*Pole pole,*" Harmand instructs them in Swahili. Slowly, slowly.

Paleoanthropologists have long viewed stone-tool production as one of the defining characteristics of the *Homo* genus and the key to our evolutionary success. Other creatures use tools, but only humans shape hard materials such as rock to suit their purposes. Moreover, humans alone build on prior innovations, ratcheting up their utility—and complexity—over time. "We seem to be the only lineage that has gone fully technological," says Michael Haslam, an independent researcher. "It isn't even a crutch. It's like an addition to our bodies."

The conventional wisdom holds that our techno dependence began to form during a period of global climate change between three million and two million years ago, when Africa's woodlands transformed into savanna grasslands. Hominins, members of the human family, found themselves at a crossroads. Their old food sources were vanishing. They had to adapt or face extinction. One lineage, that of the so-called robust australopithecines, coped by evolving huge molars and powerful jaws to process the tougher plant foods available in grassland envi-

IN BRIEF

A traditional view of human evolution holds that stone-tool technology originated with members of our genus, *Homo,* as an adaptation to shifting climate.

In this scenario, that adaptation quickly helped to establish a feedback loop that dramatically expanded brain size and technological prowess in our lineage.

Recently discovered stone tools from Kenya that date to 3.3 million years ago—long before the oldest known *Homo fossils*—have overturned this scenario.

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WORKERS DIG into the side of a hill at Lomekwi 3 in July 2016, looking for artifacts (*1*). They sift each bucket of sediment they remove, hoping to recover even the smallest fragments of interest (*2*). Every pebble is studied for signs of human modification.

ronments. Another—the larger-brained *Homo*—invented stone tools that gave it access to a wide variety of food sources, including the animals that grazed on these new plants. With the rich stores of calories from meat, *Homo* could afford to fuel an even bigger brain, which could then invent new and better tools for getting still more calories. In short order, a feedback loop formed, one that propelled our brain size and powers of innovation to ever greater heights. By one million years ago the robust australopithecines disappeared, and *Homo* was well on its way to conquering the planet.

The Lomekwi tools have smashed that scenario to pieces. Not only are they too old to belong to *Homo,* but they also predate the climate shift that supposedly kindled our ancestors' drive to create. And without any cut-marked bones or other signs of butchery at the site, it is not at all certain that the tools were used to process animal foods. What is more, such a vast expanse of time separates the Lomekwi tools from the next oldest implements on record that it is impossible to connect them to the rest of humanity's technological endeavoring, suggesting that the advent of stone tools was not necessarily the watershed moment that experts have always envisioned it to be.

These new discoveries have scientists scrambling to figure out when and how our predecessors acquired the cognitive and physical traits needed to conceptualize and fashion stone tools and to pass their craft to the next generation. If multiple lineages made tools from rock, researchers will need to rethink much of what they thought they knew about the origins of technology and how it shaped our branch of the family tree.

DAWN BREAKS GENTLY IN THE BUSH—A SLOW brightening of sky, a creeping swell of birdsong—and the team's campsite, on the bank of a dry riverbed about a mile from Lomekwi 3, comes to life. By 6:30 A.M. the workers emerge from their tents and head to the makeshift dining table for breakfast, walking along a gravel path lined with stones to deter the snakes and scorpions. Within the hour they pile into Land Cruisers and set off on a bone-rattling ride to the excavation.

The team is down one vehicle and short on seats in the remaining two, so archaeologist Hélène Roche has decided to stay at camp. Roche is an emeritus director of research at the French National Center for Scientific Research and an expert in early stone-tool technologies. She has short, sand-colored hair, and she

Map by Amanda Montañez

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dresses in desert hues. Her voice is low and crisp. Roche led the archaeological research in western Turkana for 17 years before handing the reins to Harmand and Lewis in 2011. She has returned for the second half of this expedition to see how they are faring. I remain at camp for the day to ask her about the history of work in this region.

"When I started in archaeology, we were just getting used to having stone tools at 1.8 [million years ago] at Olduvai," Roche recalls. In 1964 Kenyan paleoanthropologist Louis Leakey announced that he had found *Homo*-like fossils in association with what were then the oldest known artifacts in the world, stone tools from Tanzania's Olduvai Gorge (referred to as Oldowan tools). He assigned the fossils to a new species, *Homo habilis,* the "handy man," cementing the idea that stone toolmaking was linked to the emergence of *Homo*.

Hints that stone tools might have originated before *Homo* soon arrived, however. In the 1970s Roche, then a graduate student, discovered older Oldowan stone tools at a site in Ethiopia called Gona. When archaeologist Sileshi Semaw, now at the National Center for Research on Human Evolution in Burgos, Spain, and his colleagues eventually analyzed the tools, they reported them to be 2.6 million years old. Because no hominin remains turned up with the tools, researchers could not be sure which species made them. Semaw and his team proposed that a small-brained australopithecine species found at a different site nearby—*Australopithecus garhi*—was the toolmaker. Few were swayed by that argument, however. *Homo* was still the favorite candidate, even though, at the time, the oldest known *Homo* fossil was only 2.4 million years old. (A recent find has extended the fossil record of *Homo* back to 2.8 million years ago.)

Yet as old as they were, the Gona artifacts looked too skillfully wrought to represent humanity's first foray into stone-tool manufacturing. So did other ancient tools that began to emerge, including some from western Turkana. In the 1990s Roche found 2.3-million-year-old Oldowan stone tools at a site five miles from here known as Lokalalei 2c. She realized that in many instances, the site preserved entire knapping sequences that she could piece together like a 3-D puzzle. By refitting the Lokalalei flakes to the cores from which they were detached, Roche and her colleagues could show that toolmakers struck as many as 70 flakes from a single core. This impressive feat required an understanding of the rock shape best suited to flaking (flat on one side and convex on the other) and careful planning to maintain that shape while knapping. "You cannot imagine what it is like to hold the pieces together and reconstruct what [the toolmaker] has done and how he has done it, to go inside the prehistoric mind," she says.

It was becoming clear that the sophistication evident in the tools from Gona, Lokalalei and elsewhere could not have sprung fully formed from the minds of these knappers. Some kind of technological tradition must have preceded the Oldowan.

In 2010 far older signs of stone-tool technology came to light. Zeresenay Alemseged, now at the University of Chicago, and his colleagues reported that they had found two animal bones bearing what appeared to be cut marks from stone tools at the site of Dikika in Ethiopia. The bones dated to 3.4 million years ago, hundreds of thousands of years before the earliest known traces of *Homo*. The researchers credited the marks to *Australopithecus afarensis,* a species that was still apelike in many respects, with about as much gray matter as a chimpanzee has and a body that retained some adaptations to life in the trees—hardly the brainy, fully terrestrial hominin that researchers had traditionally expected the first butcher to be. The claims did not go unchallenged, however. Some experts countered that animals could have trampled the bones. Without the stone tools themselves, the critics argued, the Dikika scars could not qualify as tool-inflicted marks—and the question of just how far back in time technology originated remained unresolved.

1

AROUND THE TIME THE BATTLE OVER THE DIKIKA bones erupted, Harmand and Lewis began to hatch a plan to look for the older stone tools that the Dikika marks, along with the too-good-to-be-first tools from Gona and Lokalalei, implied should exist. In the summer of 2011 they set out in search of new archaeological sites on the western side of Lake Turkana.

The Turkana basin, as well as much of the Great Rift Valley in which it sits, is a paleoanthropologist's dream. Not only does it harbor an abundance of fossils and artifacts, but it preserves them in rocks that, with some sleuthing, can be dated with a relatively high degree of certainty. The region's history of volcanic eruptions and fluctuating water levels is recorded in the layers of sediment that have accumulated over eons to form a sort of layer cake. Water and wind erosion have exposed cross sections of the cake in locations throughout the basin. Tectonic activity has pushed some sections higher and other sections lower than they once were, but as long as any given exposure preserves at least a few layers of the cake, researchers can figure out where in the geologic sequence it comes from and thus how old it is.

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EXCAVATORS CHIPPED away at the sediments for weeks before finding any artifacts (*1*). The first finds were flakes produced incidentally during knapping (*2*). A volcanic ash layer called the Toroto Tuff helped to establish the age of the site (*3*).

To navigate the rough, roadless landscape, the team drives in the dry riverbeds, called *lagas,* that snake through the region, running from the lake to points west. On July 9 of that year the researchers were headed to a site where, 12 years earlier, a different team had found a 3.5-million-year-old skull of another hominin species, *Kenyanthropus platyops,* when they took the wrong branch of the Lomekwi *laga* and got lost. Climbing a nearby hillside to get a better view of the terrain, they realized that they had ended up in just the kind of place that is promising for finding ancient remains. Outcrops of soft lake sediments, which tend to preserve fossils and artifacts well, surrounded them. And the researchers knew from previous geologic mapping of the region that all the sediments along this *laga* were more than 2.7 million years old. They decided to look around.

Within a couple of hours Sammy Lokorodi, one of the Turkana members of the team, found several rocks bearing hallmarks of knapping—adjacent, scoop-shaped scars where sharp flakes had been chipped off. Could these be the older, more primitive tools that the team was looking for? Maybe. But the tools were found on the surface. A modern-day human—perhaps a passing Turkana nomad—could have made them and left them there. The researchers knew that to make a convincing case that the tools were ancient, they would have to find more of them, sealed in sediments that had lain undisturbed since their deposition, and conduct detailed geologic analyses of the site to establish the age of the artifacts more precisely. Their work had just begun.

By the time the researchers went public with their discovery, describing it in 2015 in *Nature,* they had excavated 19 stone tools from a 140-square-foot area. And they had correlated the position of the sediment layer that held the tools to layers of rock with known ages, including a 3.31-million-year-old layer of compacted volcanic ash called the Toroto Tuff and a magnetically reversed layer from a time, 3.33 million years ago, when the earth's magnetic poles switched places. They had also located the source of the raw material for the tools—a 3.33-million-year-old layer of beach containing cobbles of volcanic basalt and phonolite, along with fish and crocodile fossils that show just how much higher lake levels were back then as compared with today. Together these clues indicated that the tools dated to a stunning 3.3 million years ago—700,000 years older than the Gona tools and half a million years older than the earliest fossil of *Homo.*

The artifacts have little in common with Oldowan tools. They are far larger, with some flakes the size of a human hand. And experiments indicate that they were knapped using different techniques. Oldowan knappers favored a freehand style, striking a hammerstone held in one hand against a core held in the other, Harmand explains. The Lomekwi knappers, in contrast, would either bang a core they held in both hands against an anvil lying on the ground or place a core on the anvil and hit it with a hammerstone. The methods and finished products demonstrate an understanding of the fracture mechanics of stone but show considerably less dexterity and planning than are evident in tools from Gona and Lokalalei. The researchers had found their pre-Oldowan stone-tool tradition. They call it the Lomekwian.

NOT EVERYONE IS CONVINCED THAT THE LOMEKWI tools are as old as the discovery team claims. Some skeptics contend that the team has not proved that the artifacts originated from the sediments dated to 3.3 million years ago. Discoveries made this field season, including the knapping debris, as well as a handful of new tools recovered during excavation, may help allay those concerns. But even researchers who accept the age and the argument that the rocks were shaped by hominins are grappling with what the find means.

First, who made the tools? To date, the team has not recovered any hominin remains from the site, apart from a single, enigmatic tooth. The age and geographical location of the tools

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suggest three possibilities: *K. platyops,* the only hominin species known to have inhabited western Turkana at the time; *A. afarensis,* the species found in association with the cut-marked animal bones from Dikika; and *Australopithecus deyiremeda,* a species that was recently named, based on a partial jawbone found in Ethiopia. Either *K. platyops* or *A. afarensis* would be surprising because both those species had a brain about the size of a chimp's—not the enlarged brain researchers thought the first toolmaker would have. (*A. deyiremeda*'s brain size is unknown.)

Small brain size is not the only anatomical trait that experts did not expect to see in an ancient knapper. Paleoanthropologists thought that tool use arose after our ancestors had abandoned life in the trees to become committed terrestrial bipeds. In this scenario, only after their hands had been freed from the demands of climbing could hominins evolve the hand shape needed to make stone tools. Yet studies of *A. afarensis,* the only one of these three species for which bones below the head have been found, indicate that although it was a capable biped on the ground, it retained some traits that would have allowed it to climb trees for food or safety. Just how important was the shift away from life in the trees to life on the ground in the emergence of stone-tool technology?

The Lomekwi 3 tools are also forcing scientists to reconsider why hominins invented stone tools to begin with. Reconstruction of the paleoenvironment of the greater Lomekwi area 3.3 million years ago indicates that it was wooded, not the savanna experts thought had forged *Homo*'s stone-working skills.

Perhaps the biggest question: Why are the Lomekwi 3 tools so isolated in time? If stone-tool manufacture was the game-changing development that experts have always thought it to be, why did it not catch on as soon as it first appeared and initiate the feedback loop that expanded the brain?

Recent studies may help explain how a hominin more primitive than *Homo* could have come to make stone tools. It turns out that some of the differences in cognitive ability between hominins and other primates may not be as great as previously thought.

Observations of our closest primate cousins, for example, hint that even though they do not manufacture stone tools in the wild, they possess many of the cognitive abilities needed to do so. David Braun of George Washington University and Susana Carvalho of the University of Oxford have found that in Bossou, Guinea, wild chimps that use stones to crack open nuts understand the physical properties of different rocks. The researchers shipped assorted stones from Kenya to Bossou and made them available to the chimps for their nut-cracking activities. Despite not having prior experience with these kinds of rock, the chimps consistently selected the ones with the best qualities for the job. And experiments with captive bonobos carried out by Nicholas Toth of the Stone Age Institute in Bloomington, Ind., and his colleagues have shown that they can be trained to make sharp flakes and use them to cut rope. "I have no doubt that our apes could replicate what [Harmand and her team] have at Lomekwi, given the right raw material," Toth asserts.

Even inventing stone tools in the first place may not have required special genius. In November 2016 Tomos Proffitt, now at University College London, and his colleagues reported that they had observed wild capuchin monkeys in Brazil's Serra da Capivara National Park unintentionally making sharp stone flakes that look for all the world like Oldowan tools. Quartzite cobbles abound in the monkeys' environment, and they will often pick up one cobble and bash it against another embedded in the ground that serves as an anvil. All the bashing dislodges sharp flakes that have the hallmarks of intentionally produced stone tools, including the scooplike shape that arises from what is known as conchoidal fracturing. The monkeys ignore the flakes, however. Instead they seem to be pulverizing the quartz to eat it—they pause between strikes to lick the resulting dust from the anvil. Perhaps early hominins invented their stone flakes by accident, too, or found naturally sharp stones in their environment, and only later, once they found a good use for them, began fashioning them on purpose.

The possibility that the Lomekwi toolmakers had hands that were at once capable of knapping and climbing in trees does not seem so improbable either, once one considers what our primate cousins can manage. The modern human hand, with its short, straight fingers and long, opposable thumb, is purpose-built for power, precision and dexterity—traits we exploit every time we swing a hammer, turn a key or send a text. Yet as the observations of chimps, bonobos and capuchins show, other primates with hands built for grasping tree branches can be surprisingly dexterous. The hands of partially arboreal hominins could have been similarly clever.

In fact, recent studies of the fossilized hand bones of three small-brained hominin species from South Africa—*Australopithecus africanus, Australopithecus sediba* and *Homo naledi*—show evidence for exactly this combination of activities. All three species have curved fingers—a trait associated with climbing. Yet in other respects, their hands look like those of toolmakers. Tracy Kivell and Matt Skinner, both at the University of Kent in England, examined the internal structure of the hand bones, which reflects the loading forces sustained in life, and found a pattern consistent with that seen in hominins known to have made and used stone tools and different from the internal structure of the hand bones of chimps. "Being a good climber and a dexterous toolmaker are not mutually exclusive," Kivell says. A variety of hand shapes can make and use stone tools, she explains. The changes the human hand eventually underwent just optimized it for the job.

Friday is choma night for the Lomekwi team—roasted goat will be served for dinner. Nick Taylor of Stony Brook, a droll Brit, is taking advantage of the menu to try to figure out what purpose the Lomekwi stone tools served. This morning one of the local Turkana shepherds brought the purchased animal for slaughter. This afternoon, as the sun begins its descent and meal preparations begin, Taylor asks camp kitchen manager Alfred "Kole" Koki to try to process the carcass with replicas of the Lomekwi tools. Koki, an experienced butcher, doubts they will work. But he gamely takes a two-inch-long flake and starts slicing. He manages to skin most of the animal and carves some of the meat with the sharp-edged rocks, discarding them as they become dull, before reclaiming his steel knife to finish the job.

Taylor observes how Koki instinctively holds each flake and how long it retains its edge before Koki requests a new one. Taylor keeps the used replica flakes so that later he and his col-

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SONIA HARMAND and husband, Jason Lewis, co-direct the West Turkana Archaeological Project that discovered Lomekwi 3.

leagues can compare their damaged edges with those of the real flakes. He will also collect some of the bones to study what kind of cut marks the carving might have left on them. And he will try using the tools to cut plant materials, including wood and tubers. In addition, Taylor is looking for any residues on the Lomekwi tools that might provide clues to what they were processing.

For whatever reason the Lomekwi hominins made stone tools, their tradition does not appear to have stuck. Nearly 700,000 years separates their implements from the next oldest tools at Gona and a more recently discovered site in Ethiopia called Ledi-Geraru. Perhaps hominins did indeed have a stone-tool culture spanning that time, and archaeologists have just not found it yet. But maybe the Lomekwi stone-working was just a flash in the pan, unrelated to the Oldowan technology that followed. Even the Oldowan record is patchy and variable, showing different tool styles at different times and places, without much continuity among them. As Roche puts it, "There is not one Oldowan but Oldowans."

This pattern suggests to many archaeologists that populations in multiple lineages of hominins and possibly other primates may have experimented with stone-tool production independently, only to have their inventions fizzle out, unbequeathed to the next generation. "We used to think that once you have toolmaking, we're off to the races," observes Dietrich Stout of Emory University. But maybe with these early populations, he says, technology was not important to their adaptation, so it simply faded away.

Around two million years ago, however, something changed. The tools from this period start to look as though they were manufactured according to the same rules. By around 1.7 million years ago a more sophisticated technology arises: the Acheulean. Known for its hand ax, the Swiss Army knife of the Paleolithic, the Acheulean tradition spread across Africa and into other parts of the Old World.

Braun thinks the shift has to do with improved information transmission. Chimps appear to have what he calls low-fidelity transmission of behavior based on observational learning. It works pretty well for simple tasks: by the end of his team's six-week-long experiment with the Bossou chimps, the entire community was using the rocks the same way. The activity seemed to spread by means of a recycling behavior in which one individual, typically a juvenile, would watch another, usually an adult, use a certain type of rock to crack nuts, after which the youngster would try to use the adult's tool set to achieve the same ends.

Modern humans, in contrast, actively teach others how to do complex things—from baking a cake to flying a plane—which is a high-fidelity form of transmission. Perhaps, Braun suggests, the variability seen in the Lomekwi tools and in those of the early Oldowan is the result of lower-fidelity transmission, and the standardization of the later Oldowan and the more sophisticated Acheulean signals the development of a more effective means of sharing knowledge, one that allowed humans to ratchet up their technological complexity.

As ancient as the tools from Lomekwi 3 are, the team suspects that even older ones are out there, awaiting discovery. One day, while the rest of the team is excavating, Lewis, Lokorodi and Xavier Boës, a geologist at the French National Institute for Preventive Archaeological Research, set out to look for them. They head for an area known to have sediments older than those at Lomekwi 3, speeding up the *laga* in a cloud of dust. They are taking the same branch they meant to take on that day in 2011 when they lost their way and discovered Lomekwi 3.

When they reach their destination, they fan out, eyes trained on the ground, scanning for signs of human handiwork in a sea of rocks baked red by the sun. Before long, Lokorodi spies cobbles bearing scoop-shaped scars. In theory, they could be more than 3.5 million years old. But to make a compelling case, the researchers will have to determine whether the rocks have been shaped by humans and, if so, figure out which stratigraphic level they eroded from, pinpoint the age of that level and then find more of them undisturbed in the ground. Lewis photographs the rocks and notes their location for possible survey in the future. The team will also explore a promising area about three miles from Lomekwi 3 that has sediments dating to more than four million years ago.

Figuring out what technology came before and after Lomekwi 3 and getting a clearer picture of how the environment was shifting will be critical to elucidating the correlations among dietary change, tools and the origins of *Homo*. "Maybe the links are all the same, but everything happened earlier," Lewis offers. "The pieces have exploded, but that doesn't mean they won't reassemble."

"We know quite a lot now but not enough," Roche says of the discoveries in western Turkana. "This is only the beginning." SA

Kate Wong is a senior editor for evolution and ecology at *Scientific American*.

MORE TO EXPLORE

3.3-Million-Year-Old Stone Tools from Lomekwi 3, West Turkana, Kenya. Sonia Harmand et al. in *Nature*, Vol. 521, pages 310–315; May 21, 2015.

Wild Monkeys Flake Stone Tools. Tomos Proffitt et al. in *Nature*, Vol. 539, pages 85–88; November 3, 2016.

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CAVE TODAY KNOWN SIMPLY AS PP13B, near Mossel Bay, South Africa, sheltered humans between 164,000 and 35,000 years ago, at a time when *Homo sapiens* was in danger of dying out. These people may have been the ancestors of us all.

Photographs by Per-Anders Petterson

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WHEN THE SEA SAVED HUMANITY

Shortly after *Homo sapiens* arose, harsh climate conditions nearly extinguished our species. The small population that gave rise to all humans alive today may have survived by exploiting a unique combination of resources along the southern coast of Africa

By Curtis W. Marean

With the global population of humans well beyond seven billion, it is difficult to imagine that *Homo sapiens* was once an endangered species. Yet studies of the DNA of modern-day people indicate that, once upon a time, our ancestors did in fact undergo a dramatic population decline. Although scientists lack a precise time line for the origin and near extinction of our species, we can surmise from the fossil record that our forebears arose throughout Africa shortly before 195,000 years ago. Back then the climate was mild and food was plentiful; life was good. But around 195,000 years ago, conditions began to deteriorate. The planet entered a long glacial stage known as Marine Isotope Stage 6 (MIS6) that lasted until roughly 123,000 years ago.

A detailed record of Africa's environmental conditions during glacial stage 6 does not exist, but based on more recent, better-known glacial stages, climatologists surmise that it was almost certainly cool and arid and that its deserts were probably significantly expanded relative to their modern extents. Much of the landmass would have been uninhabitable. While the planet was in the grip of this icy regime, the number of people plummeted, and only a subset contributed to the surviving population. Geneticists debate how small this population was, but it could have been as few as several hundred individuals. Estimates of the timing of the bottleneck tend to be at around 150,000 years ago. Given the narrow genetic diversity of modern humans, it seems likely that the main progenitor population was a single group, perhaps one ethnolinguistic group, that lived in one region and then spread outward, mixing with other populations as it moved.

I began my career as an archaeologist working in East Africa

IN BRIEF

Sometime between 195,000 and 123,000 years ago, African *Homo sapiens* populations plummeted, thanks to cold, dry climate conditions that left much of the land uninhabitable. Everyone alive today is descended from people from a single region who survived this catastrophe.

The southern coast of Africa would have been one of the few spots where humans could survive during this climate crisis because it harbored an abundance of shellfish, mammals and edible plants.

Excavations of a series of sites in this region have recovered items left behind from this possible progenitor population.

The discoveries confirm the idea that advanced cognitive abilities evolved earlier than previously thought—and may have played a role in the survival of the species.

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Seaside Sanctuary
Between 195,000 and 123,000 years ago, the planet was locked in an ice age known as Marine Isotope Stage 6, rendering much of the African continent cool and arid—unsuitable for the plants and animals that *Homo sapiens* ate. Only a few regions could have supported our species, namely, those with grassland or Mediterranean scrub vegetation. The southern coast would have been a particularly plentiful oasis, thanks to three rich resources—the edible fynbos plants that grow only here; the dense shellfish beds nurtured by the Agulhas current and the Benguela upwelling of nutrient-rich cold water from the sea bottom; and the populations of large mammals living on the exposed plain.
Mediterranean scrub
Semidesert
Extreme desert
Tropical rain forest
Savanna
Scrub
Woodland
Grassland
Semidesert
Extreme desert
Mediterranean scrub
Woodland
PP13B
Agulhas current
Fynbos vegetation
PP13B
Benguela upwelling

and studying the origin of modern humans. But my interests began to shift when I learned of the population bottleneck that geneticists had started talking about in the early 1990s. Humans today exhibit very low genetic diversity relative to many other species with much smaller population sizes and geographic ranges—a phenomenon best explained by the occurrence of a population crash in early *H. sapiens*. Where, I wondered, did our ancestors manage to survive during the climate catastrophe? Only a handful of regions could have had the natural resources to support hunter-gatherers. Paleoanthropologists argue vociferously over which of these areas was the ideal spot. The southern coast of Africa, rich in shellfish and edible plants year-round, seemed to me as if it would have been a particularly good refuge in tough times. So, in 1991, I decided I would go there and look for sites with remains dating to glacial stage 6.

My search within that coastal area was not random. I had to find a shelter close enough to the ancient coastline to provide easy access to shellfish and elevated enough that its archaeological deposits would not have been washed away between 130,000 and 125,000 years ago, a period of transition when the climate warmed and sea levels surged. In 1999 my South African colleague Peter Nilssen and I decided to investigate some caves he had spotted at a place called Pinnacle Point, a promontory near the town of Mossel Bay that juts into the Indian Ocean. Scrambling down the sheer cliff face, we came across a cave that looked particularly promising—one known simply as PP13B. Erosion of the sedimentary deposits located near the mouth of the cave had exposed clear layers of archaeological remains, including hearths and stone tools. Even better, a sand dune and a layer of stalagmite capped these remnants of human activity, suggesting that they were quite old. By all appearances, we had hit the jackpot. The following year, after a local ostrich farmer built us a 180-step wood staircase to allow safer access to the site, we began to dig.

Since then, my team's excavations at PP13B and other nearby sites have recovered a remarkable record of the activities undertaken by the people who inhabited this area between approxi-

Don Foley (map), Lucy Reading-Ikkanda (globe)

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High and Dry

Finding archaeological sites dating to glacial stage 6 required searching for shelters that were close enough to the sea to allow relatively easy access to shellfish yet elevated enough that their ancient remains would not have washed away when the sea level rose 123,000 years ago. PP13B and other caves carved into the sheer cliff face of a promontory called Pinnacle Point meet those requirements and have yielded a plethora of remains dating to this critical juncture in human prehistory.

mately 164,000 and 35,000 years ago, hence during the bottleneck and after the population began to recover. The deposits in these caves, combined with analyses of the ancient environment there, have enabled us to piece together a plausible account of how the prehistoric residents of Pinnacle Point eked out a living during a grim climate crisis. The remains also debunk the abiding notion that cognitive modernity evolved long after anatomical modernity: evidence of behavioral sophistication abounds in even the oldest archaeological levels at PP13B. This advanced intellect no doubt contributed significantly to the survival of the species, enabling our forebears to take advantage of the resources available on the coast.

While elsewhere on the continent populations of *H. sapiens* died out as cold and drought claimed the animals and plants they hunted and gathered, the lucky denizens of Pinnacle Point were feasting on the seafood and carbohydrate-rich plants and large mammals that proliferated there despite the hostile climate. As glacial stage 6 cycled through its relatively warmer and colder phases, the seas rose and fell, and the ancient coastline advanced and retreated. But so long as people tracked the shore, they had access to an enviable bounty.

A COASTAL CORNUCOPIA

FROM A SURVIVAL STANDPOINT, what makes the southern edge of Africa attractive is its unique combination of plants and animals. There a thin strip of land containing the highest diversity of flora for its size in the world hugs the shoreline. Known as the Cape Floral Region, this 90,000-square-kilometer strip contains an astonishing 9,000 plant species, some 64 percent of which live only there. Indeed, the famous Table Mountain that rises above Cape Town in the heart of the Cape Floral Region has more species of plants than does the entire U.K. Of the vegetation groups that occur in this realm, the two most extensive are the fynbos and the renosterveld, which consist largely of shrubs. To a human forager equipped with a digging stick, they offer a valuable commodity: the plants in these groups produce the world's greatest diversity of geophytes—underground energy-storage organs such as tubers, bulbs and corms.

Geophytes are an important food source for modern-day hunter-gatherers, for several reasons. They contain high amounts of carbohydrate; they attain their peak carbohydrate content reliably at certain times of the year; and, unlike aboveground fruits, nuts and seeds, they have few predators. The bulbs and corms that dominate the Cape Floral Region are additionally appealing because in contrast to the many geophytes that are highly fibrous, they are low in fiber relative to the amount of energy-rich carbohydrate they contain, making them more easily digested by children. (Cooking further enhances their digestibility.) And because geophytes are adapted to dry conditions, they would have been readily available during arid glacial phases. Recent studies in South Africa show that many of these species are easy to procure and rich in calories.

The southern coast also has an excellent source of protein to offer. Just offshore, the collision of nutrient-rich cold water from the Benguela upwelling and the warm Agulhas current creates a mix of cold and warm eddies along the southern coast. This varied ocean environment nurtures diverse and dense beds of shellfish in the rocky intertidal zones and sandy beaches. Shellfish are a very high quality source of protein and omega-3 fatty acids. And as with geophytes, glacial cooling does not depress their numbers. Rather, lower ocean temperatures result in a greater abundance of shellfish. Recent research by our team has shown that a third food resource was present during these glacial phases: large-bodied mammals such as antelope and zebra. When sea levels dropped, a plain was exposed in front of the caves, and our study shows that grasslands dominated this plain, and herds of large mammals moved across these grasslands. The

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region, in short, provided an unprecedented concentration of three major food types during glacial periods.

SURVIVAL SKILLS

EVEN WITHOUT ANTELOPE, the southern coast, with its combination of calorically dense, nutrient-rich protein from the shellfish and low-fiber, energy-laden carbs from the geophytes, would have provided an ideal diet for early modern humans during glacial stage 6. Furthermore, women could obtain both these resources on their own, freeing them from relying on men to provision them and their children with high-quality food. We have yet to unearth proof that the occupants of PP13B were eating geophytes—sites this old rarely preserve organic remains—although younger sites in the area contain extensive evidence of geophyte consumption. But we have found clear evidence that they were dining on shellfish. Studies of the shells found at the site conducted by Antonieta Jerardino, then at the University of Barcelona, show that people were gathering brown mussels and local sea snails called alikreukel from the seashore. They also ate marine mammals such as seals and whales on occasion.

Previously the oldest known examples of humans systematically using marine resources dated to less than 120,000 years ago. But dating analyses performed by Miryam Bar-Matthews of the Geological Survey of Israel and Zenobia Jacobs of the University of Wollongong in Australia have revealed that the PP13B people lived off the sea far earlier than that: as we reported in 2007 in the journal *Nature,* marine foraging there dates back to a stunning 164,000 years ago. By 110,000 years ago the menu had expanded to include species such as limpets and sand mussels.

This kind of foraging is harder than it might seem. The mussels, limpets and sea snails live on the rocks in the treacherous intertidal zone, where an incoming swell could easily knock over a hapless collector. Along the southern coast, safe harvesting with sufficiently high returns is only possible during low spring tides, when the sun and moon align, exerting their maximum gravitational force on the ebb and flow of the water. Because the tides are linked to the phases of the moon, advancing by 50 minutes a day, I surmise that the people who lived at PP13B—which 164,000 years ago was located much farther inland, two to five kilometers from the water, because of lower sea levels—scheduled their trips to the shore using a lunar calendar of sorts, just as modern coastal people have done for ages. A recent study by Jan De Vynck of Nelson Mandela Uni-

Gone Shellfishing

Shellfish, which are rich in protein, are thought to have aided survival of the Pinnacle Point population because they abound year-round in the rocky intertidal zone along the southern coast of Africa (*1*). Brown mussels (*2*) have turned up in even the earliest levels of PP13B, dating to 164,000 years ago, revealing that humans began exploiting marine resources earlier than previously thought. In addition to mussels, the occupants of the Pinnacle Point sites collected various kinds of limpets as well as sea snails called alikreukel for food and gathered empty shells of helmet snails for their aesthetic appeal (*3*).

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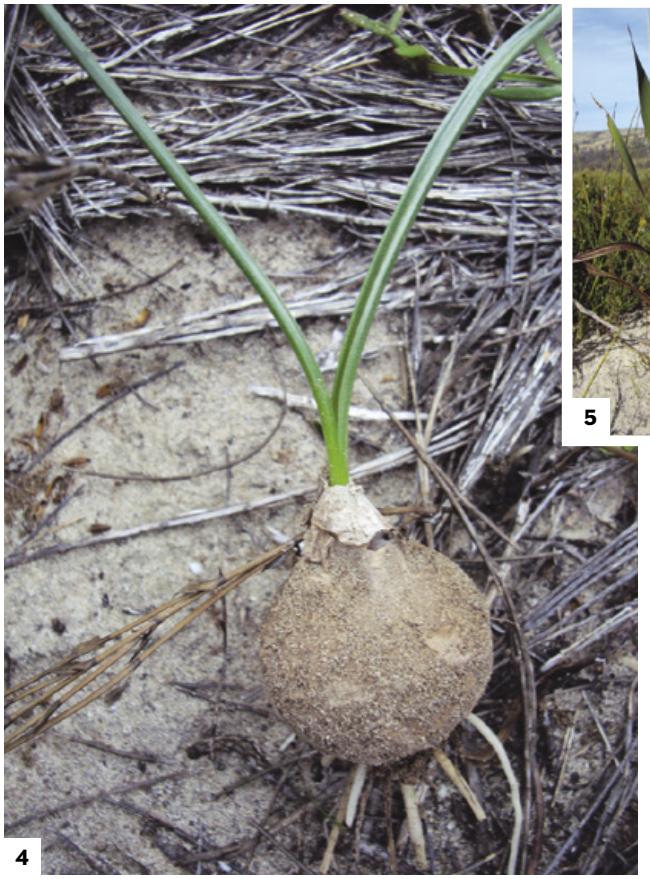

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Digging for Dinner

Geophytes, the underground energy-storage organs of certain kinds of plants (*4*), swell with edible carbohydrates at certain times of the year. The distinctive vegetation that hugs the southern coast of Africa, particularly the fynbos plants (*5*), produces especially nutritious and easily digested geophytes, which presumably served as a staple for the early modern humans who lived in this region during glacial stage 6.

versity found that skilled coastal foragers could harvest shellfish at return rates that exceed the former king of return-rate foraging—large mammal hunting!

Harvesting shellfish is not the only advanced behavior in evidence at Pinnacle Point as early as 164,000 years ago. Among the stone tools are significant numbers of "bladelets"—tiny flakes twice as long as they are wide—that are too small to wield by hand. Instead they must have been attached to shafts of wood and used as projectile weapons. Composite toolmaking is indicative of considerable technological know-how, and the bladelets at PP13B are among the oldest examples of it. But we soon learned that these tiny implements were even more complex than we thought.

Most of the stone tools found at coastal South African archaeological sites are made from a type of stone called quartzite. This coarse-grained rock is great for making large flakes, but it is difficult to shape into small, refined tools. To manufacture the bladelets, people used fine-grained rock called silcrete. There was something odd about the archaeological silcrete, though, as observed by Kyle S. Brown, now at the University of Cape Town, an expert stone tool flaker on my team. After years of collecting silcrete from all over the coast, Brown determined that in its raw form the rock never has the lustrous red and gray coloring seen in the silcrete implements at Pinnacle Point and elsewhere. Furthermore, the raw silcrete is virtually impossible to shape into bladelets. Where, we wondered, did the toolmakers find their superior silcrete?

A possible answer to this question came from another site we are excavating, Pinnacle Point Cave 5-6 (PP5-6), where one day in 2008 we found a large piece of silcrete embedded in ash. It had the same color and luster seen in the silcrete found at other archaeological deposits in the region. Given the association of the stone with the ash, we asked ourselves whether the ancient toolmakers might have exposed the silcrete to fire to make it easier to work with—a strategy that has been documented in ethnographic accounts of native North Americans and Australians. To find out, Brown carefully "cooked" some raw silcrete and then attempted to knap it. It flaked wonderfully, and the flaked surfaces shone with the same luster seen in the artifacts from our sites. We thus concluded that the Stone Age silcrete was also heat-treated.

We faced an uphill battle to convince our colleagues of this remarkable claim, however. It was archaeology gospel that the Solutrean people in France invented heat treatment about 20,000 years ago, using it to make their beautiful tools. To bolster our case, we used three independent techniques. Chantal Tribolo of the University of Bordeaux Montaigne performed what is called thermoluminescence analysis to determine whether the silcrete tools from Pinnacle Point were intentionally heated. Then Andy Herries, at the time at the University of New South Wales in Australia, employed magnetic susceptibility, which looks for changes in the ability of rock to be magnetized—another indicator of heat exposure among iron-rich rocks. Finally, Brown used a gloss meter to measure the luster that develops after heating and flaking and compared it with the luster on the tools he made. Our results, published in 2009 in *Science,* showed that intentional heat treatment was a dominant technology at Pinnacle Point by 72,000 years ago and that people there employed it intermittently as far back as 164,000 years ago. In 2012 in a study in *Nature* we showed that Pinnacle Point residents employed an entirely new technique of stone tool manufacture, called microlithic technology, far earlier than anywhere else in the world. This technology allows one to make very small, light stone weapons and represents a breakthrough in the lethality of armaments.

The process of treating by heat testifies to two uniquely modern human cognitive abilities. First, people recognized that they could substantially alter a raw material to make it useful—in this case, engineering the properties of stone by heating it, thereby turning a poor-quality rock into high-quality raw material. Second, they could invent and execute a long chain of processes. The making of silcrete blades requires a complex series of carefully designed steps: building a sand pit to insulate the silcrete, bringing the heat slowly up to 350 degrees Celsius, holding the temperature steady

COURTESY OF J. C. DE VYNCK *Center for Coastal Paleosciences, Nelson Mandela University*

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and then dropping it down slowly. Creating and carrying out the sequence and passing technologies down from generation to generation probably required language. Once established, these abilities no doubt helped our ancestors outcompete the archaic human species they encountered once they dispersed from Africa. In particular, the complex pyrotechnology detected at Pinnacle Point would have given early modern humans a distinct advantage as they entered the cold lands of the Neandertals, who seem to have lacked this technique. When combined with a new form of extreme cooperation and the advanced projectiles made possible by microlithic technology, modern humans swept out of Africa and conquered the planet [see "The Most Invasive Species of All," by Curtis W. Marean; SCIENTIFIC AMERICAN, August 2015].

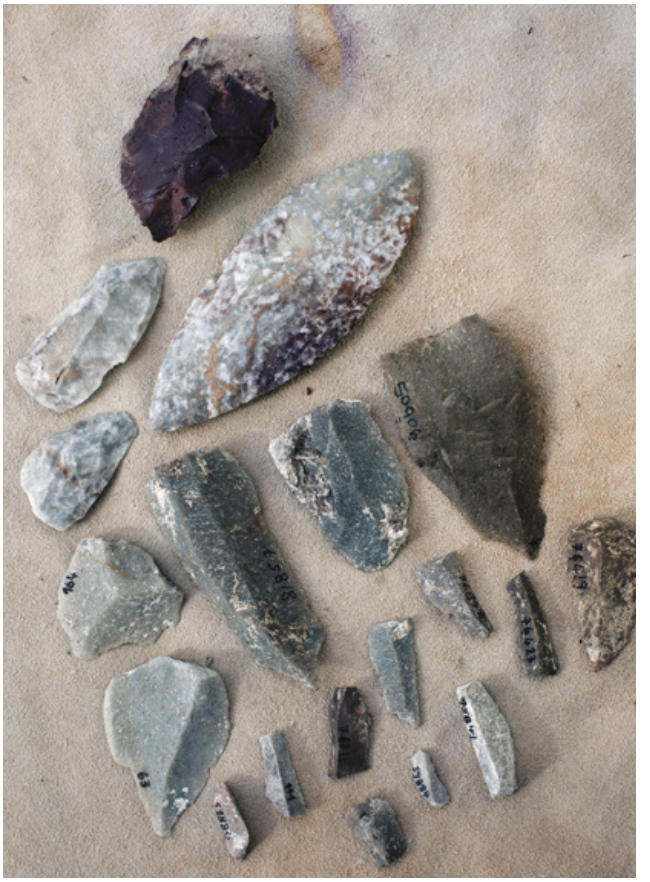
SMART FROM THE START

IN ADDITION to being technologically savvy, the prehistoric denizens of Pinnacle Point had an artistic side. In the oldest layers of the PP13B sequence, my team has unearthed dozens of pieces of red ochre (iron oxide) that were variously carved and ground to create a fine powder that was probably mixed with a binder such as animal fat to make paint that could be applied to the body or other surfaces. Such decorations typically encode information about social identity or other important aspects of culture—that is, they are symbolic. Many of my colleagues and I think that this ochre constitutes the earliest unequivocal example of symbolic behavior on record and pushes the origin of such practices back by tens of thousands of years. Evidence of symbolic activities also appears later in the sequence. Deposits dating to around 110,000 years ago include both red ochre and seashells that were clearly collected for their aesthetic appeal because by the time they washed ashore from their deepwater home, any flesh would have been long gone. I think these decorative seashells, along with the evidence for marine foraging, signal that people had, for the first time, begun to embed in their worldview and rituals a clear commitment to the sea.

The precocious expressions of both symbolism and sophisticated technology at Pinnacle Point have major implications for understanding the origin of our species. Fossils from Ethiopia show that anatomically modern humans had evolved by at least 195,000 years ago, and newly dated fossils found long ago in Morocco suggest the species may date back to 300,000 years ago. The emergence of the modern mind, however, is more difficult to establish. Paleoanthropologists use various proxies in the archaeological record to try to identify the presence and scope of cognitive modernity. Artifacts made using technologies that require outside-the-box connections of seemingly unrelated phenomena and long chains of production—like heat treatment of rock for tool manufacture—are one proxy. Evidence of art or other symbolic activities is another, as is the tracking of time through proxies such as lunar phases. For years the earliest examples of these behaviors were all found in Europe and dated to after 40,000 years ago. Based on that record, researchers concluded that there was a long lag between the origin of our species and the emergence of our peerless creativity.

But over the past 25 or so years archaeologists working at a number of sites in South Africa have found examples of sophisticated behaviors that predate by a long shot their counterparts in Europe. For instance, archaeologist Ian Watts, who works in South Africa, has described hundreds to thousands of pieces of worked and unworked ochre at sites dating as far back as 120,000 years ago. Interestingly, this ochre, as well as the pieces at Pinnacle Point, tends to be red despite the fact that local sources of the mineral exhibit a range of hues, suggesting that humans were preferentially curating the red pieces—perhaps associating the color with menstruation and fertility. Jocelyn A. Bernatchez, then at Arizona State University, thinks that many of these ochre pieces may have been yellow originally and then heat-treated to turn them red. And at Blombos Cave, located about 100 kilometers west of Pinnacle Point, Christopher S. Henshilwood of the Universities of Bergen in Norway and Witwatersrand, Johannesburg, in South Africa has discovered pieces of ochre with systematic engravings, beads made of snail shells and refined bone tools, all of which are older than 70,000 years ago. These sites, along with those at Pinnacle Point, belie the claim that modern cognition evolved late in our lineage and suggest instead that our species had this faculty at its inception.

I suspect that a driving force in the evolution of this complex cognition was strong long-term selection acting to enhance our ancestors' ability to mentally map the location and seasonal vari-



Cutting-Edge Technology

Stone tools found in PP13B include sophisticated implements such as microblades (*bottom two rows*), which would have been attached to a wood shaft to form projectile weapons. The toolmakers also appear to have heat-treated the stone to make it easier to shape—a technique that was believed to have originated much later and in France.

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Probing the Past

Continued excavation of PP13B (*shown here*) and other caves along the southern coast of Africa should reveal more about the progenitor population of humans who survived the population bottleneck and went on to colonize the globe.

ation of many species of plants in arid environments and to convey this accumulated knowledge to offspring and other group members. This capacity laid the foundation for many other advances, such as the ability to grasp the link between the phases of the moon and the tides and to learn to schedule their shellfish-hunting trips to the shore accordingly. Together the readily available shellfish and other abundant foods provided a high-quality diet that allowed people to become less nomadic, increased their birth rates and reduced their child mortality. The larger group sizes that resulted from these changes would have promoted symbolic behavior and technological complexity as people endeavored to express their social identity and build on one another's technologies, explaining why we see such sophisticated practices at PP13B.

FOLLOW THE SEA

PP13B PRESERVES a long record of changing occupations that, in combination with the detailed records of local climate and environmental change my team has obtained, is revealing how our ancestors used the cave and the coast over millennia. Modeling the paleocoastline over time, Erich C. Fisher, now at Arizona State, has shown that the conditions changed quickly and dramatically, thanks to a long, wide, gently sloping continental shelf off the coast of South Africa called the Agulhas bank. During glacial periods, when sea levels fell, significant amounts of this shelf would have been exposed, putting considerable distance—up to 95 kilometers—between Pinnacle Point and the ocean. When the climate warmed and sea levels rose, the water advanced over the Agulhas bank again, and the caves were seaside once more.

Recent research by our group shows that when the sea retreated, a grassland formed close to the caves, and the fynbos persisted north of the caves. So when the coast was moderately distant, there was an exceptionally rich confluence of food resources for people: geophytes from the fynbos, shellfish from the sea and large game animals on the grasslands. When the coast retreated farther away, people followed the sea so that they always had access to coastal foods. We recently showed in an article in *Nature* in March 2018 that people here thrived through the Toba megavolcanic eruption—it seems likely that the rich resource base made this possible.

Our excavations at PP13B have intercepted the people who may very well be the ancestors of everyone on the planet as they shadowed the shifting shoreline. Yet if I am correct about these people and their connection to the coast, the richest record of the progenitor population lies underwater on the Agulhas bank. There it will remain for the near future, guarded by great white sharks and dangerous currents. We can still test the hypothesis that humans followed the sea by examining sites on the current coast such as PP13B and PP5-6. But we can also study locations where the continental shelf drops steeply and the coast was always near—investigations that Fisher is currently running on the eastern coast of Africa in Pondoland.

The genetic, fossil and archaeological records are reasonably concordant in suggesting that the first substantial and prolonged wave of modern human migration out of Africa occurred around 70,000 years ago. But questions about the events leading up to that exodus remain. We still do not know, for example, whether at the end of glacial stage 6 there was just one population of *H. sapiens* left in Africa or whether there were several, with just one ultimately giving rise to everyone alive today.

Such unknowns are providing my team and others with a very clear and exciting research direction for the foreseeable future: our fieldwork needs to target the other potential progenitor zones in Africa during that glacial period and expand our knowledge of the climate conditions just before that stage. We need to flesh out the story of these people who eventually pushed out of their refuge, filled up the African continent and went on to conquer the world. SA

Curtis W. Marean is Foundation Professor at the Institute of Human Origins at Arizona State University and honorary professor at the Center for Coastal Palaeoscience at Nelson Mandela University in South Africa. He studies the origins of modern humans, the prehistory of Africa, paleoclimates and paleoenvironments, and animal bones from archaeological sites. Marean is particularly interested in human occupation of coastal ecosystems. He is the principal investigator for the South African Coast Paleoclimate, Paleoenvironment, Paleoecology, Paleoanthropology (SACP4) project, funded by the National Science Foundation.

MORE TO EXPLORE

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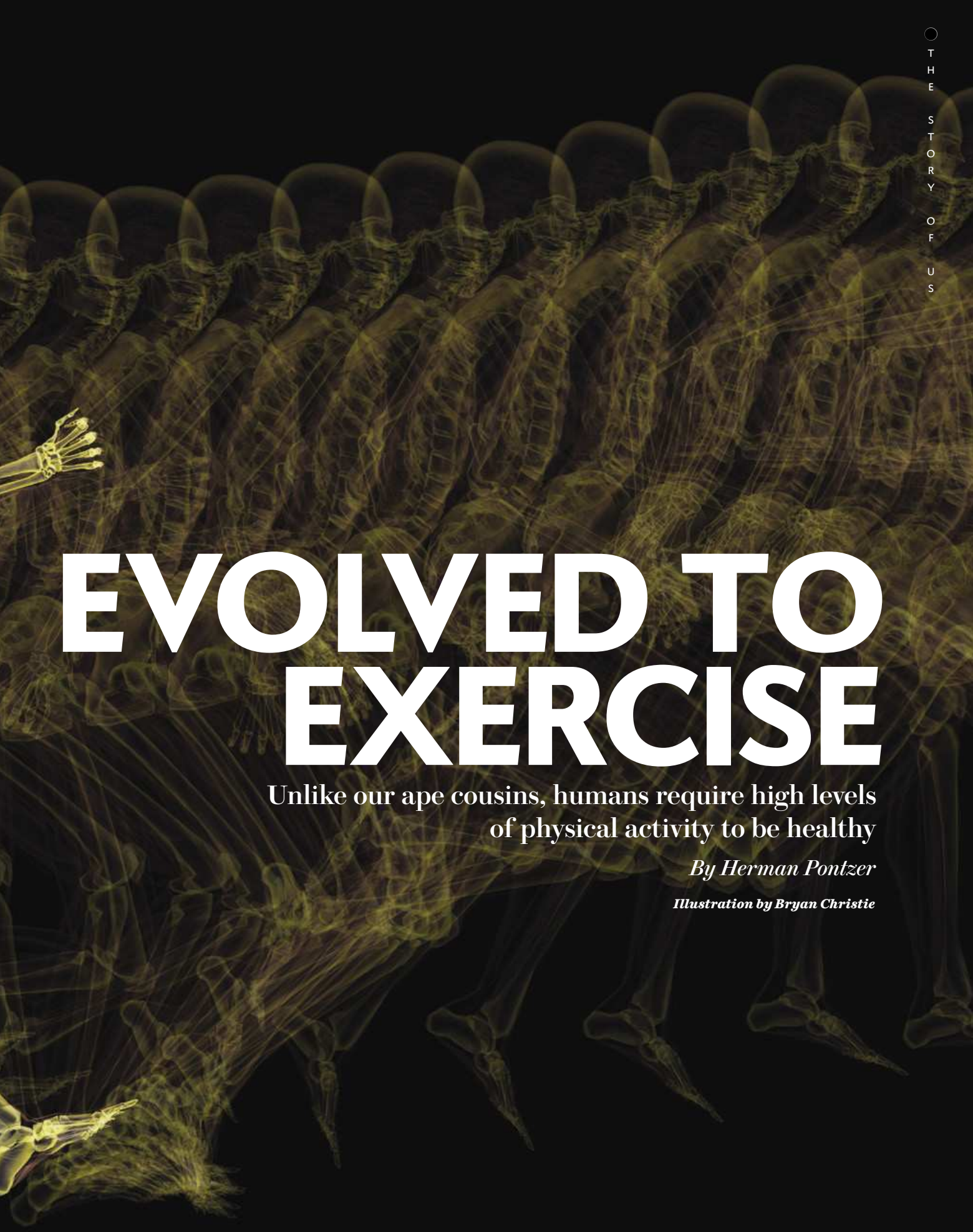

EVOLVED TO EXERCISE

Unlike our ape cousins, humans require high levels of physical activity to be healthy

By Herman Pontzer

Illustration by Bryan Christie

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IN THE PREDAWN DAMP OF A UGANDAN RAIN FOREST NEARLY 20 YEARS AGO, I stared up through the crowded canopy at a party of eight chimpanzees sleeping overhead. Our team of three researchers and two field assistants had woken up an hour before, wiggling into rubber boots and hastily assembling backpacks before setting out on muddy trails by headlamp. Now at our destination, the lights were off, and we stood there silently, submerged in a black ocean of forest, the surface 30 meters above, listening to the chimps chuffing and shifting in their leafy nests.

IN BRIEF

Our closest living relatives, the great apes, have habitually low levels of physical activity yet suffer no ill health effects from being lazy.

Humans have evolved to require far higher levels of exercise to be healthy.

New research reveals that as human anatomy and behavior shifted over the past two million years, so, too, did physiology.

Our physiology adapted to the intensive physical activity that hunting and gathering requires.

As a young Ph.D. student studying human and ape evolution, I was in Kibale National Park that summer to measure how much chimpanzees climb each day. It seemed to me that the energy spent climbing might be a critical factor in chimpanzee ecology and evolution, shaping their anatomy to maximize climbing efficiency, thus sparing calories for reproduction and other essential tasks. Months earlier, while mulling over summer research plans from the comfort of my desk at snowy Harvard University, I envisioned chimpanzees waging a heroic struggle for existence, working hard on a daily basis to eke out a living. But as I settled into the rhythm of fieldwork that summer, following chimpanzees from dawn to dusk, I came to a very different conclusion: chimpanzees are lazy. Only recently have I come to appreciate what ape idleness tells us about human evolution.

People are drawn to apes because we see so much of ourselves in them. It is not just that we share more than 97 percent of our DNA with orangutans, gorillas, chimpanzees and bonobos. Apes are clever, use tools, fight and make up, and sneak off to have sex. Some will kill their neighbors over turf and hunt other species for food. The kids learn from their mothers, wrestle and play with one another, and throw tantrums. And the further back in time we go in the fossil record, the more apelike our ancestors look. No species alive today is a perfect model of the past—all lineages change over time. But living apes provide the best chance to see where we came from and to understand how much of us is ancient and unchanged.

And yet it is the differences, rather than the similarities, between humans and apes that are casting new light on the way our bodies work. Discoveries from fossil excavations, zoos and laboratories around the world are revealing just how radically our bodies changed over the past two million years. For decades researchers have known that this last chapter of our evolution was marked by major anatomical and ecological changes—among them, ballooning brain size, hunting and scavenging, increasingly complex stone tools and larger body size. But they have generally assumed that these were changes in shape and behavior, not in the fundamental function of our cells. Current advances are overturning that view, showing how humans have changed physiologically as well. Unlike our ape cousins, we have evolved a dependency on physical activity. We must move to survive.

PARADISE LOST

A TYPICAL DAY'S AGENDA for a chimpanzee in the wild reads like the daily schedule for lethargic retirees on a Caribbean cruise, though with fewer organized activities. Wake up early, crack of dawn, then off to breakfast (fruit). Eat until you are stuffed, and next find a nice place for a nap, maybe some light grooming. After an hour or so (no rush!), go find a sunny tree with figs and gorge yourself. Maybe go meet some friends, a bit more grooming, another nap. Around five o'clock have an early dinner (more fruit, maybe some leaves), then it is time to find a nice sleeping tree, build a nest and call it a night. Sure, there are frenetic pant-hoot choruses when the fruit is really great and the occasional scuffle or monkey hunt, and the alpha male needs to carve some time out every day to thrash a few victims or display mightily. But in general, chimpanzee life is pretty mellow.

It is not just chimps. Orangutans, gorillas and bonobos also lead the sorts of seemingly idle lives that children's fables and high school drug programs warn you about. Great apes spend eight to 10 hours a day resting, grooming and eating before knocking off in the evening for nine or 10 hours of sleep per night.

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LOUNGING AROUND: A mountain gorilla family relaxes in Rwanda. Great apes remain healthy at low activity levels.

DAVID CAYLESS Getty Images

Chimps and bonobos walk about three kilometers a day, and gorillas and orangutans travel even less. And the climbing? As I discovered that summer, chimpanzees climb about 100 meters a day, the caloric equivalent of another 1.5 kilometers of walking. Orangutans do about the same, and although their ascent has yet to be measured, gorillas surely climb less.

In humans, these activity levels would be a recipe for serious health problems. Our taking fewer than 10,000 daily steps is associated with increased risk of cardiovascular and metabolic disease. U.S. adults typically clock about 5,000 steps, which contributes to the alarming rates of type 2 diabetes, affecting one in 10 Americans, and heart disease, which accounts for a quarter of all deaths in the U.S. By these lights, apes should be in trouble. Converting their walking and climbing to steps per day for comparison across species, we see that great apes rarely accumulate even the modest step counts seen among sedentary humans and never approach the human benchmark of 10,000 steps a day.

Then there is all the sitting and resting. In humans, sitting at a desk or in front of the television for protracted periods is associated with increased risk of disease and a shorter life span, even among people who exercise. Worldwide, physical inactivity is arguably on par with smoking as a health risk, killing more than five million people annually. Among Scottish adults, those watching more than two hours of television a day had a 125 percent increase in cardiac events such as heart attack or stroke. A study in Australian adults reported that every hour accumulated watching television shortened life expectancy by 22 minutes. I will save you the math: bingeing all 63½ hours of *Game of Thrones* in its entirety will cost you one day on this planet.

Yet chimpanzees and other apes remain remarkably healthy at their habitually low levels of physical activity. Even in captivity, diabetes is rare, and blood pressures do not increase with age. Despite having naturally high cholesterol levels, chimpanzee arteries do not harden and clog. As a result, chimps do not develop humanlike heart disease or have heart attacks from occluded coronary arteries. And they stay lean. In 2016 I worked with Steve Ross at Lincoln Park Zoo in Chicago and a team of collaborators to measure metabolic rates and body composition in zoo-living apes across the U.S. The results were eye-opening: even in captivity, gorillas and orangutans average only 14 to 23 percent body fat and chimpanzees less than 10 percent, on par with Olympic athletes.

Among our primate cousins, we humans are clearly the odd ape out. Somehow humans evolved to require much higher levels of physical activity for our bodies to function normally. Sitting for hours on end, grooming and napping (or watching the tube) have gone from standard practice to a health risk. When did we trade the low-key existence of our fellow apes for a more strenuous way of life and why? Fossil discoveries are helping to piece the story together.

BRANCHING OUT

OUR LIMB OF THE PRIMATE FAMILY TREE, the hominins, split from that of chimpanzees and bonobos about six million or seven million years ago, near the end of Miocene geologic time period. Until fairly recently, there were few hominin fossils recovered from the earliest portion of the lineage. Then, in quick succession during the 2000s, paleoanthropologists working in Chad, Kenya and Ethiopia reported finds of three hominins from this critical period: *Sahelanthropus, Orrorin* and *Ardipithecus.*

Each of these early hominins is distinct from any of the living apes in the anatomical details of their cranium, teeth and skeleton. Nevertheless, aside from walk-

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ing on two legs, it appears these species lived a very apelike existence. Their molars were similar in size and sharpness to chimpanzees, with somewhat thicker enamel, suggesting a mixed diet of fruit and other plant foods. *Ardipithecus,* found in 4.4-million-year-old deposits in Ethiopia and by far the best known early hominin, had long arms, long, curved fingers and grasping feet, indicative of a life spent partly in the trees. New biomechanical analyses, led by my City University of New York graduate student Elaine Kozma, show that *Ardipithecus* had evolved changes in its pelvic anatomy to permit fully upright, energetically efficient walking without compromising the ability to power itself into the canopy. Our early ancestors were clearly comfortable in two worlds, on the ground and in the trees.

BINGEING ALL 63½ HOURS OF *GAME OF THRONES* WILL COST YOU ONE DAY ON THIS PLANET.

From about four million to two million years ago the hominin record is dominated by the genus *Australopithecus,* with at least five species recognized today, including the famous "Lucy" and her kin. Anatomical changes in the lower limb point to improved walking ability and more time on the ground compared with earlier species. The grasping foot is gone in *Australopithecus,* the big toe in line with the others, and the legs are longer, the same ratio of leg length to body mass that we see in living humans. Analyses of the pelvis by Kozma, together with recent work on the fossilized footprints from Laetoli in Tanzania, indicate that this creature had an effectively modern gait. Long arms and fingers tell us these hominins were still regularly in the trees to forage and perhaps to sleep. Analyses of the wear patterns on their teeth suggest *Australopithecus* species primarily ate plant foods, just as the earliest hominins did before them and living apes do today. Based on their large, thick-enameled molars, *Australopithecus* diets most likely leaned more on harder and more fibrous foods, particularly when preferred foods were not available.

The evolution of an upright, striding bipedal gait in these early hominins is important, indicating a different approach for navigating their landscape. Covering more ground for fewer calories might have enabled these species to expand their range and thrive in less productive habitats than apes today. There are other notable and intriguing changes, too, such as the loss of big, sharp canines in males, which seem to reflect changes in social behavior. Yet the plant-based diet and retained climbing adaptations tell us their foraging ecology and daily activity remained quite apelike. Distances traveled per day were probably modest, with lots of time spent resting and digesting bellyfuls of fibrous plant food. It is unlikely they needed, or often got, their 10,000 steps a day.

Some two million years ago the telltale signs of curious or clever hominins experimenting with new ideas and approaches began to emerge. In 2015 Sonia Harmand of Stony Brook University and her team recovered large, unwieldy stone tools, some weighing more than 30 pounds, from 3.3-million-year-old sediments on the western shore of Lake Turkana in Kenya. In the past 15 years excavations at 2.6-million-year-old sites in both Ethiopia and Kenya have found stone tools associated with fossilized animal bones bearing the unmistakable gouges and scrapes of butchery. By 1.8 million years ago cut-marked bones and stone tools were the norm, and it was not just the sick and injured animals that fell prey to these hominins. Analyses of butchered bones at Olduvai Gorge in Tanzania show that prime-aged ungulates were targeted. Just as important, unlike every hominin before, by 1.8 million years ago hominins had expanded outside of Africa into Eurasia, from the foothills of the Caucasus Mountains to the rain forests of Indonesia. Our predecessors had jumped the ecological fence and were capable of thriving nearly anywhere.

Forget the tales of some clandestine meeting in the Garden of Eden or of Prometheus doling out fire. It was this million-year dalliance with stones and meat and the development of a hunting-and-gathering strategy that pushed our lineage away from the other apes, changing things irrevocably. This tectonic shift marked the evolutionary emergence of us, the genus *Homo*.

FOOD FOR THOUGHT

IN ECOLOGY AND EVOLUTION, diet is destiny. The foods animals eat do not just shape their teeth and guts but their entire physiology and way of living. Species evolved to eat foods that are abundant and stationary need not roam too far or be too clever to fill up; grass does not hide or run away. Eating foods that are hard to find or capture means more travel, often coupled with increased cognitive sophistication. For instance, fruit-eating spider monkeys in Central and South America have larger brains and travel five times farther every day than the leaf-obsessed howler monkeys that share their forests. Carnivores on the African savanna travel three times farther a day than the herbivores they hunt.

Shifting from the pure gathering lifestyle of apes and early hominins to the hunting-and-gathering strategy that marks the genus *Homo* had major ramifications. It made these social primates even more tightly knit. Relying on meat requires cooperation and sharing—and not just because you cannot kill or eat a zebra by yourself. Meat is difficult to obtain, and sharing more predictable plant foods is what allows hunting and gathering to work. Hunter-gatherer popula-

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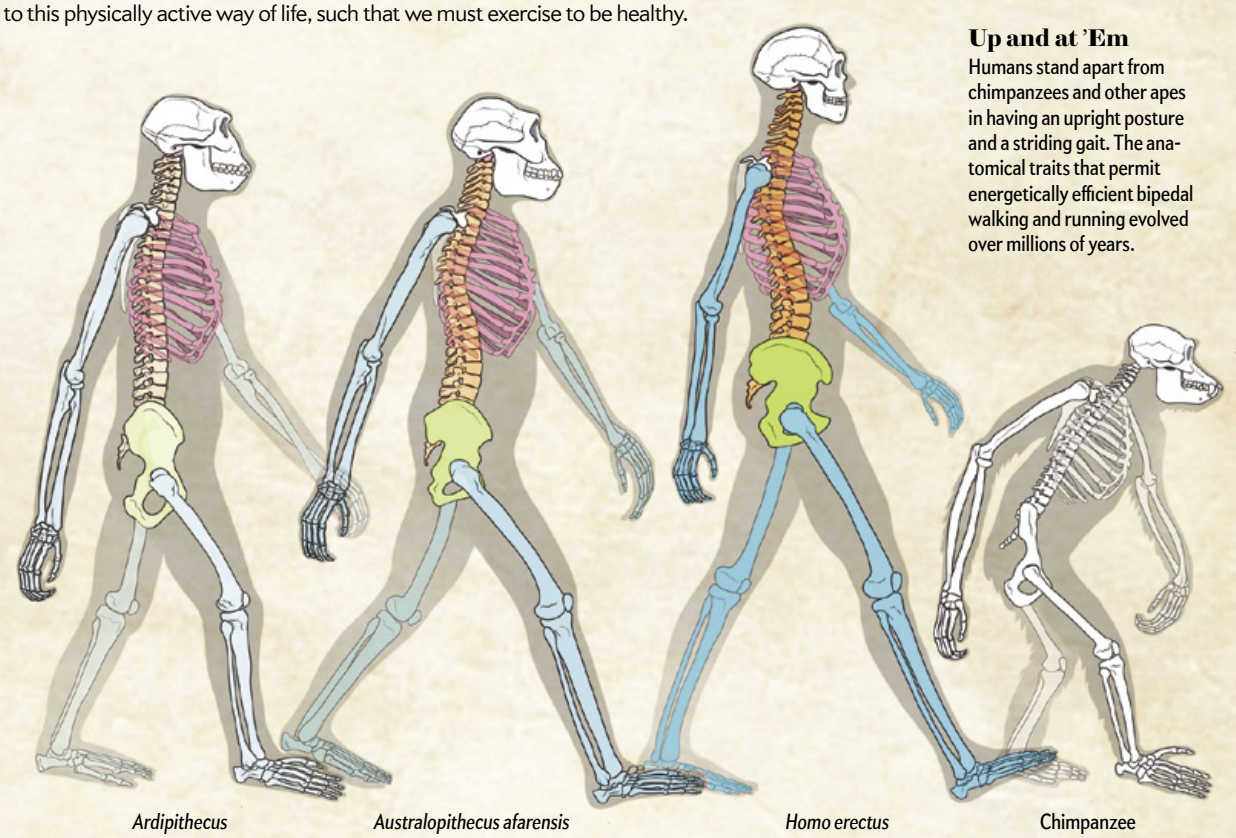
Built to Move

As hominins evolved anatomical changes that facilitated upright walking (*shown*), they were able to cover more ground for fewer calories, allowing them to expand into new habitats. The subsequent advent of hunting further increased activity levels of hominins, requiring them to travel farther to find food. Our physiology has adapted to this physically active way of life, such that we must exercise to be healthy.

Up and at 'Em

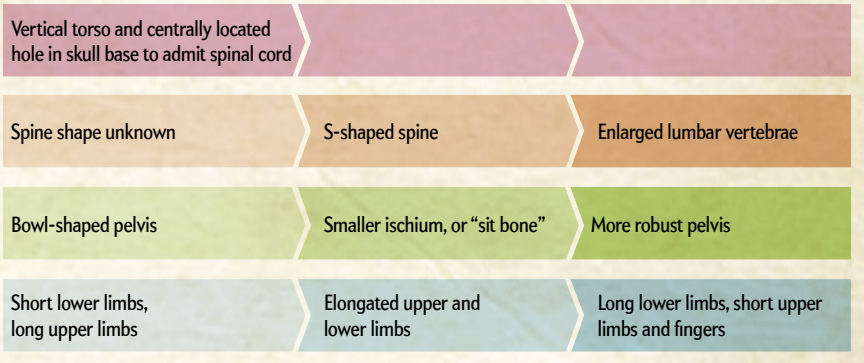
Humans stand apart from chimpanzees and other apes in having an upright posture and a striding gait. The anatomical traits that permit energetically efficient bipedal walking and running evolved over millions of years.



Ardipithecus | *Australopithecus afarensis* | *Homo erectus* | Chimpanzee

Piecemeal Evolution

Early human ancestors, including *Ardipithecus* and *Australopithecus*, walked on two legs yet also retained adaptations to climbing in the trees, ate a plant-based diet like today's apes do and lived exclusively in Africa. By 1.8 million years ago *Homo* had evolved modern body proportions, adopted a dietary strategy of hunting and gathering, and spread out of Africa into Eurasia.


Vertical torso and centrally located hole in skull base to admit spinal cord
Spine shape unknown
S-shaped spine
Enlarged lumbar vertebrae
Bowl-shaped pelvis
Smaller ischium, or "sit bone"
More robust pelvis
Short lower limbs, long upper limbs
Elongated upper and lower limbs
Long lower limbs, short upper limbs and fingers

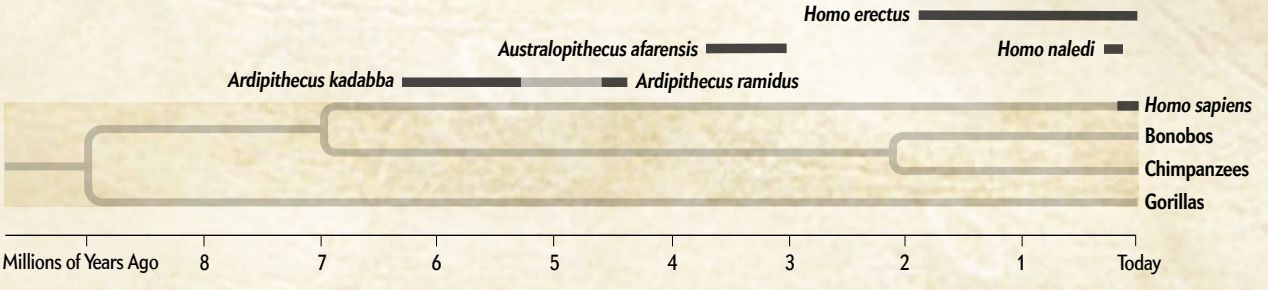


Illustration by Mesa Schumacher

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tions today get roughly half their daily calories from plants. Recent analyses of the food trapped inside their fossilized dental calculus show that even Neandertals, masterful hunters and avatars of vegetable-boycotting Paleo diet bros everywhere, ate a balanced diet, with plenty of plants, including grains.

Hunting and gathering also put an evolutionary premium on intelligence. Technological innovation and creativity meant more calories and better odds of reproduction. Social intelligence would have proved invaluable, as coordination and communication became ingrained parts of the hominin strategy. Discoveries by Alison Brooks of George Washington University, Rick Potts of the Smithsonian National Museum of Natural History and their colleagues at the site of Olorgesailie Basin in Kenya, published in 2018, show that by 320,000 years ago, hominin cognition had blossomed into the kind of sophistication seen in modern humans, with black and red pigments for visual expression and long-distance trade networks for premium stone tool material. The age of these finds corresponds well with the oldest *Homo sapiens* fossils found to date, reported in 2017 from the 300,000-year-old site of Jebel Irhoud in Morocco.

EXERCISE IS NOT OPTIONAL; IT IS ESSENTIAL.

Moreover, hunting and gathering required hominins to work harder for their food. Simply moving up the food chain means food is harder to find; there are a lot more plant calories on the landscape than animal calories. Hunter-gatherers are remarkably active, typically covering nine to 14 kilometers a day on foot—about 12,000 to 18,000 steps. Work that David Raichlen of the University of Arizona, Brian Wood, now at the University of California, Los Angeles, and I have done with the Hadza hunter-gatherer population in northern Tanzania shows that men and women in that group log more physical activity in a day than Americans typically get in a week and travel three to five times farther every day than any of the great apes. Early members of our genus, without the benefit of technological innovations such as the bow and arrow, might have been even more active. In a landmark paper in 2004, Dennis Bramble of the University of Utah and Daniel Lieberman of Harvard argued that our genus evolved to run prey to exhaustion, pointing to a number of features in the *Homo erectus* skeleton that appear to reflect endurance running.

The steady increases in brain size and technological complexity over the past two million years seem to accumulate like a snowball rolling downhill, but any impression of momentum is an illusion. Evolution has a great memory but no plans. In 2015 Lee Berger of the University of the Witwatersrand in South Africa and his team announced their discovery of hundreds of fossils of *Homo naledi,* a new species recovered from deposits deep in the Rising Star Cave system in South Africa, dated to between 236,000 and 335,000 years old. With a brain size only 10 percent larger than *Australopithecus* and a body size similar to early *Homo,* this hominin appears to represent a lineage within our genus that stalled out in the early Pleistocene, persisting quite happily for more than a million years without the continued increase in brain size seen in other *Homo* species. *H. naledi* is an important reminder that evolution is not trying to get anywhere. We were not inevitable.

SHARKS ON THE SAVANNA

NO TRAIT EVOLVES IN ISOLATION: brains must fit snugly inside their skulls, teeth inside their jaws; muscles, nerves and bones must function harmoniously. Behavioral traits are no different. When a behavioral strategy—such as hunting and gathering—becomes the norm, physiology adapts to accommodate and even depend on it.

Take vitamin C, for instance. Early mammals evolved a multistep process to make this crucial nutrient on their own, a cascade involving several genes that remains functional in rodents, carnivores and many other mammals. Tens of millions of years ago our primate ancestors became so fixated on eating fruits rich in vitamin C that making their own became an unnecessary cost. Their physiology adapted to their behavior, with mutations accumulating in the gene needed in the final step of synthesis. Consequently, today's anthropoid primates—monkeys, apes and humans—cannot make vitamin C. Without it in our diets, we get scurvy and die.

Further afield, yet closer to home, is the evolution of a specialized form of breathing called ram ventilation in several species of sharks and scombrid fish (the group that includes tuna and mackerel). These lineages evolved highly active foraging behavior, swimming nonstop day and night. Their anatomy and physiology adapted, using the constant forward motion to ram water into their mouths and past their gills. This change eliminated the need to pump water past the gills, leading to the evolutionary loss of the associated gill musculature. This loss saved energy but left these species vulnerable to suffocation. If they stop moving, they die.

Although we have long known that exercise is good for us humans, we are only beginning to appreciate the myriad ways our physiology has adapted to the physically active way of life that hunting and gathering demands. Nearly every organ system is implicated, down to the cellular level. Some of the most exciting work in this area has focused on the brain. For one thing, our brain has evolved to get less sleep, even in societies without artificial lighting or other modern nighttime distractions. Humans around the globe—whether it is the Hadza on the African savanna, the Tsimane horticulturalists in the Amazonian rain forest or urbanites in New York—clock about seven hours of sleep a night, far less than apes.

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Raichlen and his colleagues have shown that our brain has evolved to reward prolonged physical activity, producing endocannabinoids—the so-called runner's high—in response to aerobic exercise such as jogging. Raichlen and others have even argued that exercise helped to enable the massive expansion of the human brain and that we have evolved to require physical activity for normal brain development. Exercise causes the release of neurotrophic molecules that promote neurogenesis and brain growth, and it is known to improve memory and stave off age-related cognitive decline.

Our metabolic engines have evolved to accommodate increased activity as well. Humans' maximum sustained power output, our VO_{2max}, is at least four times greater than that of chimpanzees. This increase stems largely from changes in our leg muscles, which are 50 percent bigger and have a much greater proportion of "slow-twitch" fatigue-resistant fibers than the leg muscles of other apes. We also have more red blood cells to carry oxygen to working muscles. But the adaptations to exercise appear to go even deeper, accelerating the rate with which our cells function and burn calories. My work with Ross, Raichlen and others has shown that humans have evolved a faster metabolism, providing fuel for increased physical activity and the other energetically costly traits that set humans apart, including bigger brains.

All of this evidence points toward a new way of thinking about physical activity. Since the sweaty spandex excitement of the 1980s, exercise has been sold as a way to lose weight or as a health-conscious buffet item to add to our lifestyle, like oat bran muffins. But exercise is not optional; it is essential, and weight loss is probably the one health benefit it largely fails to deliver. Our bodies are evolved to require daily physical activity, and consequently exercise does not make our bodies work *more* so much as it makes them work *better*. Research from my lab and others has shown that physical activity has little effect on daily energy expenditure (Hadza hunter-gatherers burn the same number of calories every day as sedentary Westerners), which is one reason exercise is a poor tool for weight loss. Instead exercise regulates the way the body spends energy and coordinates vital tasks.

Recent advances in metabolomics have shown that exercising muscles release hundreds of signaling molecules into the body, and we are only beginning to learn the full extent of their physiological reach. Endurance exercise reduces chronic inflammation, a serious risk factor for cardiovascular disease. It lowers resting levels of the steroid hormones testosterone, estrogen and progesterone, which helps account for the reduced rate of reproductive cancers among adults who exercise regularly. Exercise may blunt the morning rise in cortisol, the stress hormone. It is known to reduce insulin insensitivity, the immediate mechanism behind type 2 diabetes, and helps to shuttle glucose into muscle glycogen stores instead of fat. Regular exercise improves the effectiveness of our immune system to stave off infection, especially as we age. Even light activity, such as standing instead of sitting, causes muscles to produce enzymes that help to clear fat from circulating blood.

No wonder populations such as the Hadza do not develop heart disease, diabetes or the other maladies that afflict industrial countries. But we do not need to cosplay as hunter-gatherers or run marathons to reap the benefits of a more evolutionarily informed life. The lesson from groups such as the Hadza, Tsimane and others is that volume matters more than intensity. They are on their feet and moving from sunrise until dusk, racking up more than two hours of physical activity a day, most of it as walking. We can emulate these same habits by walking or biking instead of driving, taking the stairs, and finding ways to work and play that keep us off our butts. A recent study of Glaswegian postal workers shows us what this can look like. These men and women were not committed athletes but were active throughout the day, handling the mail. Those who got 15,000 steps or spent seven hours a day on their feet (numbers similar to what we see with the Hadza) had the best cardiovascular health and no metabolic disease.

While we are at it, we might take other lessons for living well from groups like the Hadza. Beyond the copious amounts of exercise and whole food diets, daily life for these cultures is full of fresh air, friendships and family. Egalitarianism is the rule, and economic inequality is low. We do not know exactly how these factors affect the health of hunter-gatherers, but we know their absence contributes to chronic stress in the developed world, which can promote obesity and disease.

Embracing more physically active life habits would be easier if we did not have to wrestle with the 400-pound gorilla in our head. Like vitamin C for our anthropoid ancestors, exercise was unavoidable and plentiful during the last two million years of hominin evolution. There was no need to seek it out, no evolutionary pressure to lose the ancient, simian weakness for gluttony and sloth. Today, as masters of our environments, we are giving our inner apes too much say in how the modern world is engineered: filling up on easy food, bingeing *The Walking Dead* instead of actually walking, sitting for hours at our desks grooming one another on social media. We are fascinated when we see ourselves in great apes, but we should worry when we see them in us. Underneath the surface, we are more different than we seem. SA

Herman Pontzer is an associate professor of evolutionary anthropology at Duke University. He studies how evolution has shaped human physiology and health.

MORE TO EXPLORE

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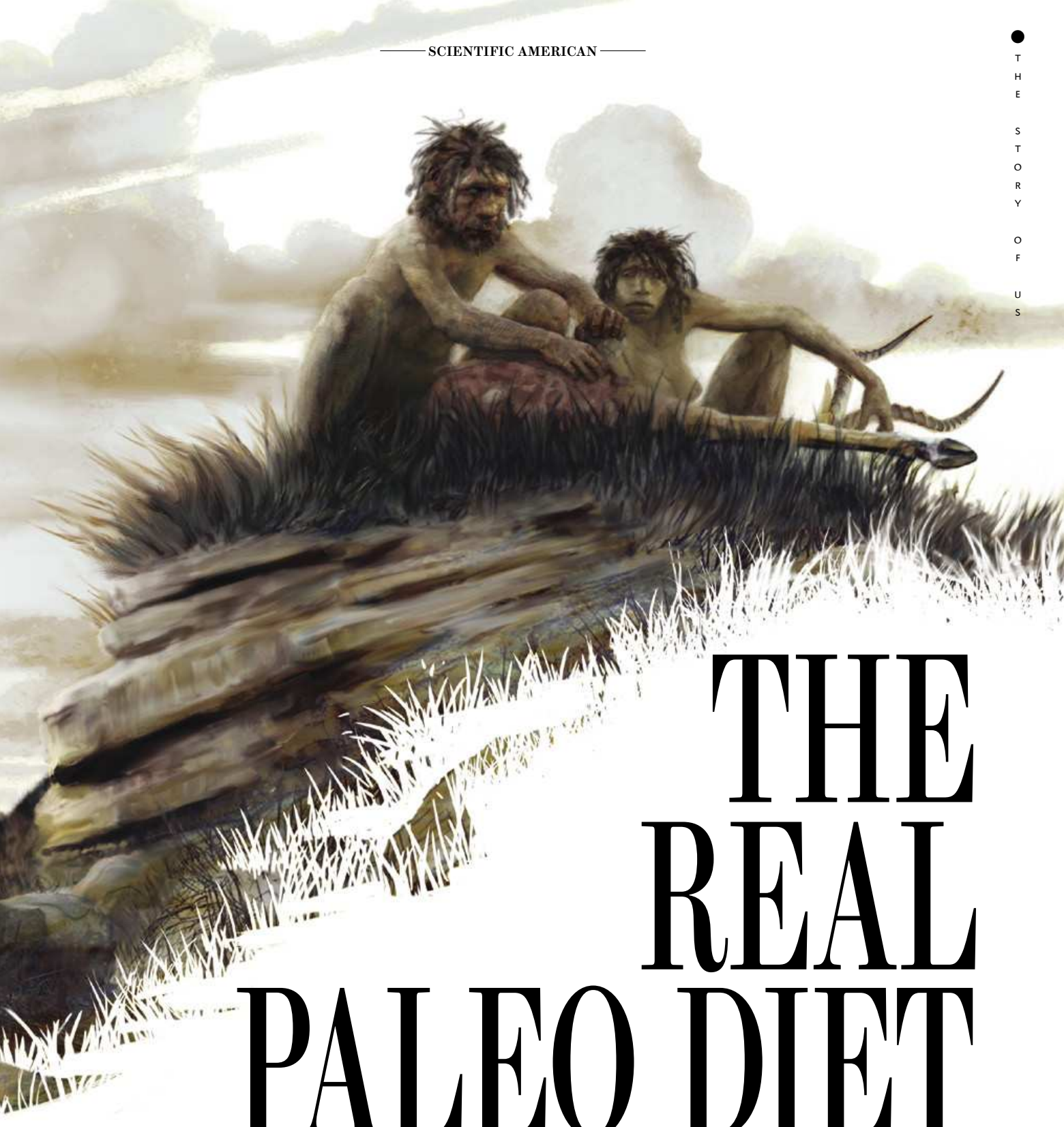

THE REAL PALEO DIET

Microscopic wear patterns on fossil teeth reveal what our ancestors ate—and provide insights into how climate change shaped human evolution

By Peter S. Ungar

Illustration by Jon Foster

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LATE ONE EVENING IN 1990 AT THE KETAMBE RESEARCH STATION IN INDONESIA'S Gunung Leuser National Park, I sat transcribing notes by the light of a kerosene lamp in my hut on the banks of the Alas River. Something was bothering me. I had come to gather data for my dissertation, documenting what and how the monkeys and apes there ate. The idea was to relate those observations to the sizes, shapes and wear patterns of their teeth. Long-tailed macaques have large incisors and blunt molars—teeth built for eating fruit, according to the received wisdom. But the ones I had been tracking for the past four days seemed to eat nothing but young leaves. I realized then that relations between tooth form and function are more complicated than the textbooks suggest and that the sizes and shapes of an animal's teeth do not dictate what it eats. This might sound like an esoteric revelation, but it has key implications for understanding how animals—including humans—evolved.

IN BRIEF

Paleontologists have traditionally assumed that the sizes and shapes of an animal's teeth dictate its diet. But food availability—which changes seasonally and over larger timescales—is an even bigger factor in what an animal chooses to eat. **Analyses of microscopic use wear** and chemical traces of food on fossil teeth are going beyond conventional studies of tooth form to reveal what human ancestors truly ate. **The diet findings,** along with paleoenvironmental data, provide fresh insights into how climate change shaped human evolution.

I am a paleontologist, and I earn a living reconstructing the behaviors of extinct species from their fossilized remains. Specifically, I work to discern how animals in the past obtained food from their surroundings and thus how environmental change triggers evolution. That year at Ketambe shaped my way of thinking about primates and the larger community of life that surrounds them. I began to see the biosphere—the part of our planet that harbors life—as a giant buffet of sorts. Animals belly up to the sneeze guard with plates in hand to pick from items available in a given place, at a given time. Each species' place in the forest, and in nature, is defined by the choices it makes.

Teeth play a role in food choice—you need the right utensils. But I learned at Ketambe that availability is even more important. The macaques ate leaves because that is what nature laid out on the biospheric buffet at that time and place. Their diet changed over the course of the year as leaves unfurled, flowers bloomed and fruits ripened with the passing seasons. I began to imagine how changes in food availability over centuries, millennia or longer could affect what a species eats.

Most paleontologists are not used to thinking about life in the past this way. Our field has a long tradition of inferring function from form by assuming that nature selects the best tools for whatever job an organism has to do. If form always followed function, however, macaques would not eat leaves. But how can we detect food choices in the fossil record?

I have spent decades doing exactly that by studying microscopic wear patterns on fossil teeth, including those of a number of human ancestors. Other researchers have analyzed the chemical signatures of food in fossil teeth for dietary clues. These "foodprints," as I call them, reveal the kinds of foods individuals actually ate and have given us a much richer picture of the past than tooth shape alone. Together with insights from the paleoenvironmental record, these findings have allowed us to test some leading hypotheses about the impact of climate change on human evolution. The results refine the classic explanation for how our branch of the human family tree succeeded where others did not.

LIEM'S PARADOX

OBSERVATIONS OF LIVING ANIMALS have revealed numerous creatures that eat foods other than the ones to which they are adapted. While I was at Ketambe, Melissa Remis, now at Purdue University, was gathering diet data on gorillas at Bai Hokou, a lowland rain forest site in the Central African Republic's Dzanga-Ndoki National Park. At that time, most researchers thought that gorillas were dietary specialists that ate stems, leaves and the pith of nonwoody plants such as wild celery. Pioneering gorilla researcher Dian Fossey and others had shown as much in the high-altitude cloud forests of the Virunga Mountains in Uganda and Rwanda. It made sense. Gorillas have very specialized teeth and guts—sharp-crested molars well suited to shearing tough plant parts and a massive

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hindgut to host microorganisms that help to digest cellulose in fibrous foods. Besides, there was little else to eat at those elevations.

The Virunga mountain gorillas were actually a small, marginal population of just a few hundred individuals living in an extreme habitat, however. What about the 200,000 gorillas living 1,000 miles to the west in the lowland rain forests of the Congo Basin? The gorillas at Bai Hokou told a different story. They seemed to prefer soft, sugary fruits. In fact, Remis saw gorillas walk half a mile or more, right past edible leaves and stems, to get to a fruiting tree. Fibrous foods seemed to dominate their diet only when favored fruits were unavailable. But western lowland gorillas were skittish compared with their cousins in the Virunga Mountains, limiting the amount of data Remis could collect. Some researchers questioned whether gorillas could actually prefer fruits, given their teeth and guts.

There is an old joke: "What do you feed a 400-pound gorilla? Anything it wants." How can we know what a gorilla wants to eat? After Remis returned home from Bai Hokou, she went to the San Francisco Zoo to ask the gorillas themselves. She offered the captive apes a variety of foods, from sweet mango to bitter tamarind, sour lemon and, of course, tough celery. The zoo gorillas clearly preferred sugary, fleshy fruits to tough, fibrous foods, regardless of what their teeth and guts suggested they should eat. This finding confirmed that although gorillas are adapted to the most mechanically and chemically challenging foods they have to eat, these are not their favored foods. Perhaps, then, gorillas in the Virunga Mountains eat tough, fibrous foods year-round not because they prefer them but because they can—and must, given the limited options on the biospheric buffet at such high elevations. Indeed, nearby mountain gorillas that live at lower altitudes prefer to eat fruit when it is available.

A preference for foods other than those to which one is adapted is common enough in the animal kingdom to merit a term for the phenomenon: Liem's paradox. The late Karel Liem of Harvard University observed the paradox first in 1980 in Minckley's cichlid, a freshwater fish endemic to the valley of Cuatro Ciénegas in northern Mexico. One form of this fish has flat, pebblelike teeth in its throat that are seemingly perfectly suited for cracking hard-shelled snails. Yet members of this group swim right past those snails when softer foods are available. Why would an animal evolve teeth specialized for less preferred, rarely eaten items? So long as the hard-object specialization does not preclude consumption of softer foods, it can leave an animal more options when it needs them. The paradox, then, is not so much that individuals avoid the foods to which they are adapted but that specialized anatomy can lead to a more generalized diet.

Other primates exemplify Liem's paradox, including the gray-cheeked mangabey monkeys of Uganda's Kibale National Park. Mangabeys have flat, thickly enameled molars that seem to be specialized for crushing hard, brittle foods. But day after day, month after month, even year after year, Joanna Lambert, now at the University of Colorado Boulder, watched them eat soft, fleshy fruits and young leaves, just like the thinner-toothed red-tailed guenon monkeys that lived alongside them. Then, in the summer of 1997, everything changed. The forest was reeling from an especially severe drought brought on by an El Niño event. Fruits were scarce, leaves were wilting and the monkeys were hungry. The mangabeys ate more bark and hard seeds, but the guenons did not. The mangabeys' specialized teeth and jaws allowed them to fall back on mechanically challenging foods. Even if such adaptations are needed only once or twice in a generation, that can be just what the animals require to get through the lean times.

Specialized anatomy can also relate to preferred foods, though. Sooty mangabeys in Ivory Coast's Taï National Park, for instance, have thick tooth enamel and strong jaws, and they actually prefer hard foods.

ALAIN HOULE

GRAY-CHEEKED MANGABEYS have flat, thickly enameled molars that appear to be specialized for crushing hard foods. But they only fall back on these foods when the soft fruits and leaves they prefer are unavailable.

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Much of their foraging time is devoted to scouring the forest floor for seeds of the *Sacoglottis* tree, which have casings that resemble peach pits. Scott McGraw of Ohio State University argues that this practice allows them to avoid competing for food with the 10 other primate species that live alongside them. Just as gorillas vary in how often they eat mechanically challenging foods, some mangabeys eat them all the time, and others do so only on rare occasions.

Examples such as these show that primate food choice is complex and depends not just on teeth but also on availability, competition and personal preference. Tooth form can tell us something about what an animal in the past was capable of eating and the most challenging foods its ancestors had to contend with. But for insights into food choices among options that were available on the biospheric buffet, we need foodprints.

TOOTH FORM CAN TELL US SOMETHING ABOUT WHAT AN ANIMAL IN THE PAST WAS CAPABLE OF EATING AND THE MOST CHALLENGING FOODS ITS ANCESTORS HAD TO CONTEND WITH. BUT FOR INSIGHTS INTO FOOD CHOICES AMONG OPTIONS THAT WERE AVAILABLE ON THE BIOSPHERIC BUFFET, WE NEED FOODPRINTS.

Dental microwear, the microscopic scratches and pits that form on a tooth's surface as the result of its use, is a commonly studied type of foodprint. Species that tend to shear or slice tough foods, such as grass-grazing antelopes or meat-eating cheetahs, get long, parallel scratches as opposing teeth slide past one another and abrasives between them are dragged along. Species that crush hard foods, such as nut-eating Taï mangabeys or bone-crunching hyenas, tend to have cratered microwear surfaces, covered in pits of various sizes and shapes.

Because those marks typically wear away and are overwritten in a matter of days, we can learn something about the variety, and perhaps even the proportions, of foods eaten if we consider teeth of individuals sampled at different times and places. The microwear patterns of Kibale mangabeys typically resemble those of soft-fruit eaters, with wispy scratches and fine pits, although a few specimens are more heavily pitted. The teeth of mangabeys from Taï, in contrast, have much more cratered surfaces on average. Despite similar tooth form in the two species, foodprints distinguish them as predicted, based on observations of their diets.

ANCIENT MENUS

WITH MICROWEAR PATTERNS from living animals whose dietary habits are known from firsthand observation to guide us, scientists can use microwear on fossil teeth to infer what extinct species ate on a daily basis and gain insight into their food choices. To that end, my colleagues and I have put a lot of effort into analyzing the microwear of human fossils. Our work has generated surprising results.

The human family tree has many branches. Today *Homo sapiens* is the only human species alive, but once upon a time, multiple human species, or hominins, shared the planet. Why our lineage survived when others went extinct is an enduring question. My own foray into this mystery began when I set out to study the diet of members of one of these extinct branches, a group of species belonging to the genus *Paranthropus*. *Paranthropus* lived in eastern and southern Africa between about 2.7 million and 1.2 million years ago, during the Pleistocene epoch. None of its species gave rise to us; rather they were evolutionary experiments that walked alongside our own early ancestors. *Paranthropus* had big, flat, thick-enameled premolars and molars, heavy jaws, and the telltale bony ridges and scars that come from having massive, powerful chewing muscles. These traits are clearly dietary specializations for extreme chewing, so these species seemed to be ideal candidates for microwear analysis. If my collaborators and I could not figure out what they ate, then we had little hope of reconstructing diets of other fossil hominins with less distinctive jaws and teeth.

Paleoanthropologist John Robinson was the first to try to reconstruct the diet of *Paranthropus,* back in 1954. Robinson believed that the large, flat and thickly enameled premolars and molars of *Paranthropus robustus* from South Africa had evolved for grinding plant parts, such as shoots and leaves, berries and tough wild fruits. Chipping on those teeth suggested to him that *P. robustus* ate grit-laden roots and bulbs. The late Phillip Tobias of the University of the Witwatersrand, Johannesburg, saw things differently, arguing in the 1960s that the chips occurred during consumption of hard foods rather than gritty ones. At the time, Tobias was describing a new species of *Paranthropus* from East Africa, *Paranthropus boisei*. On first seeing its skull, he is famously reported to have said, "I have never seen a more remarkable set of nutcrackers."

The idea of a hominin that specialized in nut cracking was born. *Paranthropus* stood in sharp contrast to early *Homo* fossils found in the same sedimentary deposits, with their daintier teeth and jaws, larger brain and emerging stone tool kit for processing food. Researchers came up with a tidy explanation for the differences, dubbed the savanna hypothesis. As grasslands began to spread across Africa, our ancestors came to an evolutionary fork in the road. *Paranthropus* went one way, evolving to specialize on hard, dry savanna plant parts, such as seeds and roots. Early *Homo* went another direction, becoming increasingly versatile, with a more flexible diet that

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included meat. That dietary flexibility is why we are here today and *Paranthropus* is gone, according to the theory. It was a compelling story, and early microwear studies by Frederick Grine of Stony Brook University in the 1980s showed that the teeth of *P. robustus* do have more microwear pits than those of its own predecessors, seemingly confirming that this cousin of ours specialized in hard, brittle foods.

But in 2005, when my then postdoctoral fellow Rob Scott and I looked again at *P. robustus* microwear using newer technology, another part of the story began to emerge. Yes, *P. robustus* specimens had more pitted, complex microwear surfaces on average, but some of the specimens we studied had less pitted, simpler textures. In fact, microwear in *P. robustus* varied a lot, suggesting that while some ate hard foods in the days before they died, others did not. To put it another way, the specialized anatomy of *P. robustus* did not mean it was a dietary specialist. This was not a new idea. David Strait, now at Washington University in St. Louis, and Bernard Wood of George Washington University had the year before speculated that *Paranthropus* may well have been an ecological generalist with a flexible diet, based largely on indirect evidence. But our work provided direct evidence for Liem's paradox among the hominins.

A bigger surprise came in 2008, when my colleagues and I looked at the microwear textures of *P. boisei*. This was Tobias's nutcracker, the species with the largest teeth, heaviest jaws and thickest enamel of all the hominins. I expected *P. boisei*'s teeth to have microwear akin to that of the sooty mangabey's, cratered like the surface of the moon. They did not. Surface after surface had wispy scratches running every which way. Not only were these critters not hard-object specialists, but their microwear showed no sign at all of hard foods. The nutcracker hypothesis seemed to fall like a house of cards in a stiff wind. So what was *P. boisei* eating with those big, flat teeth? That would have to wait on another set of foodprints: carbon isotope ratios.

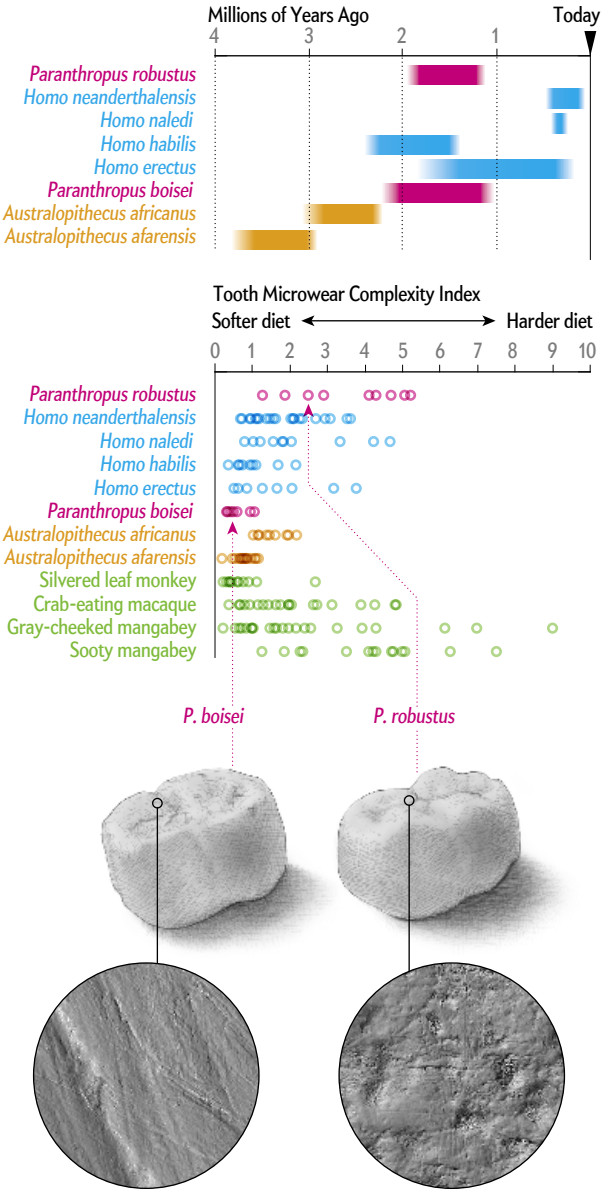
Distinctive chemical signatures of foods that provide the raw materials used to build the body are sometimes preserved in teeth. Like microwear, these chemical clues can be read and decoded. For example, compared with trees and bushes, tropical grasses have a higher proportion of carbon atoms with seven neutrons rather than the usual six; the teeth of animals that eat tropical grasses have predictably more "heavy" carbon as a result.

Carbon isotope ratios of *P. robustus* teeth indicate a diet dominated by tree and bush products but with a hearty helping of tropical grasses or sedges. This finding is consistent with a broad-based diet. But *P. boisei* shows a very different pattern, with carbon isotope ratios suggesting that grasses or sedges made up at least three quarters of its diet.

This result came as a surprise to many paleoanthropologists. A cowlike hominin? Surely no self-respecting member of our family tree would earn its living eating grass! But it made sense to me. These species debuted just as grasslands were spreading across eastern and southern Africa, and the biospheric buffet table was becoming covered in turf. If *P. boisei* was grinding grass or sedge products with its big, flat teeth and powerful jaws rather than crushing hard, brittle foods, that should leave exactly the microwear texture pattern

Foodprints

Microscopic scratches and pits form on teeth as a result of their use. Studies of these microwear patterns in living animals show that species that chew soft and tough foods such as grass, for example, get long, parallel scratches on their teeth; those that crush hard and brittle foods such as nuts get pits. Paleontologists have inferred the diet of extinct human species, including *Paranthropus robustus* and *Paranthropus boisei,* based on the microwear textures on fossil teeth.



Previous studies based on tooth form concluded that *P. robustus* ate tough plants and that *P. boisei* specialized in cracking nuts. Microwear analysis, however, reveals that *P. robustus* had a complex pattern of pits and scratches indicative of a dietary generalist. *P. boisei,* for its part, had none of the pits one would expect to see in a nutcracker. Subsequent chemical analyses indicated that *P. boisei* ate mostly grasses or sedges.

PETER S. UNGAR (*data and microwear simulations*)

Illustration by Portia Sloan Rollings (teeth), Graphics by Jen Christiansen

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JOHN R. FOSTER *Science Source*

my colleagues and I found. Such a diet would also explain why *P. boisei* wore down its molars so quickly.

You would never know it by just looking at the shapes of their huge, flat teeth, but foodprints suggest that the two *Paranthropus* species used their specialized anatomy in different and unexpected ways. Like the Kibale mangabeys, *P. robustus* seems to have had a generalized diet that included some hard objects. But for *P. boisei,* the relation between teeth and diet seems to have been very different from anything we see in primates today. Big, flat teeth are far from ideal for shredding grass, but one works with what one has. And so long as a grinding platform is better than what hominins had before, it would be selected for even if it is not optimal for the task at hand.

Microwear of our direct ancestors—those in the *Homo* genus—points to a decidedly different dietary strategy. My colleagues and I have looked at two early species: the more "primitive" *Homo habilis,* a smaller-brained hominin that retained some features related to life in the trees, and *Homo erectus,* a larger-brained hominin committed to the ground. Our samples are small because microwear requires pristine teeth, and there are just not that many of them. But they show an interesting pattern. Compared with *Australopithecus afarensis,* its putative ancestor, and *P. boisei,* which lived alongside it, *H. habilis* has a somewhat broader range of microwear textures, from complex pitted surfaces to simple scratched ones. The finding hints that *H. habilis* ate a wider range of foods than either its predecessors or its contemporaries. Its successor *H. erectus* has even more variable microwear textures, perhaps suggesting a broader diet still.

DIVERGING DIETS: Whereas *Paranthropus boisei* (*1*) specialized in eating grasses or sedges, its contemporary *Homo habilis* (*2*) appears to have had a broader diet.

These results fit neatly with a leading model of how climate change shaped human evolution that has superseded the savanna hypothesis. Work on climate data from deep ocean cores in the mid-1990s by geologist Nicholas Shackleton showed there was more to the story of climate change than the savanna hypothesis supposed. Conditions did become cooler and drier over the long term, but there were also short-term climate swings, and those swings became more and more intense over the course of human evolution.

Rick Potts of the Smithsonian Institution reasoned that this unstable climate pattern should favor more versatile species, including hominins—an idea that became known as the variability selection hypothesis. Pleistocene Africa was no place to be a picky eater. For Potts, it was not so much the spread of savanna grasses but the need for flexibility that drove human evolution. In this light, *Homo*'s larger brain and stone tools for processing a variety of foods make sense. They would have allowed our ancestors to survive increasingly intense environmental swings and to keep up as nature more quickly swapped items on and off the biospheric buffet. The increasing variation in microwear complexity from *A. afarensis* to *H. habilis* to *H. erectus* just might be direct evidence of variability selection.

Potts's idea has held up pretty well in the two decades since he first presented it, although others have built on it, and new details have emerged about how changes to Earth's landscapes and to its orbit around the sun have combined to create the conditions under which humans evolved. For example, in 2009 Mark Maslin of University College London and Martin

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Trauth of the University of Potsdam in Germany suggested that climate swings filled and emptied the spreading lakes in eastern Africa, disrupting life in the rift basins. This flux may have led to fragmentation and dispersal of hominin populations, fueling human evolution. The ability to pursue a more variable diet would have aided survival in such turbulent times.

APPETITE AND EVOLUTION

ALTHOUGH THE AVAILABLE EVIDENCE allows scientists to paint a plausible picture of how early hominins adapted to their changing world, we can only do so with the broadest of brushstrokes. The biggest challenge to understanding how climate change drives evolution is matching specific climate events in the past to changes in the fossil record.

Local environments react to global and even regional climate change in different ways, and our fossil record is simply not complete enough to tell exactly where and when particular species appeared and disappeared. We can be off by 1,000 miles and 100,000 years or more. We might be able to tie the extinction or evolution of a given species to a massive, catastrophic event in Earth's history, such as the asteroid impact in the Yucatán Peninsula that killed off the dinosaurs 66 million years ago. But the climate-related events we associate with human evolution are very different—repeated cycles of cool-dry conditions followed by warm-wet ones. The fact that hominins were probably flexible species capable of adjusting to a broad range of habitats and the foods available within them further obscures the picture. Our best shot at understanding how hominins responded to changing environments thus lies in the more recent past, in places that are exceptionally well studied.

Research published by Sireen El Zaatari of the University of Tübingen in Germany, Kristin Krueger of Loyola University Chicago and their colleagues over the past several years shows how this approach might work. Their studies of the microwear of Neandertals and the anatomically modern humans that supplanted them in Eurasia allow us to revisit the long-standing mystery of this replacement from a fresh perspective. Neandertals ruled Europe and western Asia between about 400,000 and 40,000 years ago. Then they were gone. Paleoanthropologists have been debating what happened and why for more than a century, and even today there is little consensus.

Although popular science often tells a tale of brutish Neandertals living in near-glacial conditions, swaddled in animal hides and gorging lustfully on mammoth and woolly rhinoceros meat, it was not always like that. Neandertals inhabited a wide range of habitats, from cold, dry steppes to warmer, wetter woodlands, and conditions varied over time and space. Recent studies of their molars show that Neandertals living in more wooded or mixed settings had complex pitted microwear, suggesting that they ate more hard, brittle and perhaps abrasive plant foods. Neandertals that dwelled on the open steppes, in contrast, have less complex molar microwear, which El Zaatari and her colleagues argue reflects a less variable diet composed primarily of soft meat. Krueger, for her part, found differences in incisor microwear between the two groups; she thinks the differences stem from the steppe Neandertals having used their incisors to aid in processing animal hides and the forest Neandertals having eaten a greater variety of foods. Intriguingly these differences hold whether one considers earlier Neandertals or later ones. It seems that Neandertals were flexible feeders with diets that tracked to habitat and associated food availabilities.

The pattern is different, though, for anatomically modern people living in Europe during the last ice age. There is not much difference in molar microwear between those from open habitats and those who occupied habitats containing a mix of open and wooded vegetation, whether one considers earlier or later individuals. Perhaps early modern humans were better able to acquire their preferred foods than Neandertals were when faced with environmental change.

FOOD FOR THOUGHT

STUDIES OF EARLY HUMAN DIETS bear on what people today should eat to be healthy—though perhaps not in the manner popularly envisioned. "Paleolithic diet" gurus argue that we should eat the kinds of foods our ancestors evolved to eat. Many chronic degenerative diseases have been linked to a mismatch between our diets and the fuels our bodies were "designed" to burn, they contend. And it certainly cannot hurt to remind ourselves every now and again that our distant forebears did not eat corn dogs or milkshakes.

That does not mean that we should look to follow a specific Paleolithic diet, however. Foodprints teach us that early hominin diets varied over time and space and that we mostly likely evolved to be flexible eaters, driven by ever changing climates, habitats and food availability. In other words, there was no single ancestral human diet for us to replicate. Dietary versatility allowed our ancestors to spread across the planet and find something to eat on all of Earth's myriad biospheric buffets. It was the key to our evolutionary success. SA

Peter S. Ungar is a paleontologist at the University of Arkansas. His research focuses on diet and feeding adaptations in living and fossil primates, including human ancestors. His most recent book is *Evolution's Bite* (Princeton University Press, 2017).

MORE TO EXPLORE

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NEEDLE IN

A new technique for identifying tiny fragments of fossilized bone is helping to answer key questions about when, where and how human species interacted with one another

By Thomas Higham and Katerina Douka

Photographs by Christoffer Rudquist

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FOSSIL SCRAPS may include precious human remains—the trick is picking them out.

THE HAYSTACK

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IT IS ALWAYS A RELIEF TO ARRIVE AT Denisova Cave in southern Siberia. After a bumpy 11-hour drive southeast from Novosibirsk, across the steppe and through the foothills of the Altai Mountains, the field camp suddenly appears around a bend in the dirt road, and all thought of the long journey evaporates. Steep-sided valleys, swift-running rivers and the traditional wood houses of the local Altai people dominate the landscape; golden eagles soar overhead. A couple of hundred meters away, the limestone cave itself, perched high above the Anui River, beckons with the promise of some of the most exciting research underway in the field of human origins.

BONE FRAGMENT from Denisova Cave in Siberia is the latest specimen to be identified as a member of the human/great ape family using zooarchaeology by mass spectrometry (ZooMS).

Denisova Cave is at the center of a revolution in scientists' understanding of how our ancestors in the Paleolithic, or Old Stone Age, behaved and interacted. Our species, *Homo sapiens,* originated in Africa hundreds of thousands of years ago. When it eventually began spreading into Europe and Asia, it encountered other human species, such as the Neandertals, and shared the planet with them for millennia before those archaic species disappeared. Scientists know these groups encountered one another because people today carry DNA from our extinct relatives—the result of interbreeding between early *H. sapiens* and members of those other groups. What we do not yet know and are eager to ascertain is when and where they crossed paths, how often they interbred and how they might have influenced one another culturally. We actually have quite a few important archaeological sites from this transitional period that contain stone tools and other artifacts. But many of these sites, including Denisova, lack human fossils that are complete enough to attribute to a particular species on the basis of their physical traits. That absence has hindered our ability to establish which species made what—and when.

Now a technique for identifying ancient bone fragments, known as zooarchaeology by mass spectrometry (ZooMS), is finally allowing researchers to start answering these long-standing questions. By analyzing collagen protein preserved in these seemingly uninformative fossil scraps, we can identify the ones that come from the human/great ape family and then attempt to recover DNA from those specimens. Doing so can reveal the species they belong to—be it Neandertal, *H. sapiens* or something else. What is more, we can carry out tests to determine the ages of the fragments.

Directly dating fossils is a destructive process—one has to sacrifice some of the bone for analysis. Museum curators are thus usually loath to subject more complete bones to these tests. But they have no such reservations with the scraps.

The ability to directly date fossils found in association with artifacts is especially exciting with regard to

IN BRIEF

During the middle and later parts of the Stone Age, *Homo sapiens* spread out of Africa into Eurasia. Subsequently, archaic human groups across the region, including the Neandertals and Denisovans, disappeared.

Researchers are keen to understand the nature and extent of interactions among these groups during this transition. But many of the relevant archaeological sites from this period lack fossils that can be attributed to one species or another based on their anatomy.

Now a combination of techniques is allowing scientists to comb through large quantities of unidentified bone scraps and pick out human remains that can be dated and genetically sequenced. Already this method has yielded insights into interspecies dynamics.

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Denisova and other sites we know sheltered multiple human species in the past. A number of researchers have argued that symbolic and decorative artifacts, which are proxies for modern cognitive abilities, are unique to *H. sapiens*. Others maintain that Neandertals and other species made such items, too, and may have even passed some of their traditions along to the *H. sapiens* they met. The ability to identify and date these fossil fragments means researchers can begin to reconstruct the chronology of these sites in far greater detail and elucidate a critical chapter of human prehistory.

MISSION IMPOSSIBLE

RUSSIAN ARCHAEOLOGISTS have been excavating Denisova Cave since the 1980s. But it was an announcement in 2010 that put the site on the map. That year scientists at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, reported on the results of their genetic analysis of a bone found at Denisova in 2008. The DNA they obtained from the fossil—a bit of finger bone—revealed a previously unknown type of hominin, or member of the human family, one that was as closely related to Neandertals as we are. The bone was from a young girl, initially dubbed "X woman," who belonged to a group of people that scientists now refer to as Denisovans. Since then, a handful of other hominin bones and teeth have been discovered among the excavated remains, both Denisovan and Neandertal.

Those discoveries at Denisova illustrated the powerful information that can be gleaned from fossils using modern genetic approaches, telling us not only about the presence of hitherto unknown species but also about the nature of their interaction with us. We know from genetic analysis, for instance, that Neandertals and modern humans interbred at least three times over the past 100,000 years and that Neandertals and Denisovans, as well as moderns and Denisovans, also mixed. As a result, the long-held view that *H. sapiens* moved out of Africa and simply wiped out such archaic populations has, in the blink of an eye, given way to a more complex scenario of interbreeding and gene flow between groups—a "leaky replacement" model of modern human origins. Yet most of the fossils at Denisova are so incomplete that we cannot discern which ones might belong to a human species. And the site has been notoriously difficult to date.

We got involved in the Denisova project in 2012 through our expertise in chronology, particularly the use of radiocarbon dating to establish time frames for archaeological sites. For material from the Middle and Upper Paleolithic periods (broadly the time spanning 250,000 to 40,000 and 40,000 to 10,000 years ago, respectively), dating is hugely important because the sites themselves often lack distinctive tool types that are associated with tightly defined periods. We are working to provide a robust chronology at Denisova and other Paleolithic locations in Eurasia.

We were both at the site in 2014 attending a meeting of the Denisova team when we came up with an idea that we thought might help us build a more nuanced picture of the interactions that occurred among our species, Neandertals and Denisovans. One thing that was apparent at Denisova was that all the known hominin remains were absolutely tiny, just three to five

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SCIENTISTS INSPECT archaeological deposits in Denisova Cave before taking samples for ZooMS analysis and radiocarbon dating.

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Whose Bone Is It, Anyway?

With ZooMS, researchers can assign bone fragments to their proper taxonomic group. ZooMS analyzes collagen protein preserved in bone. An enzyme cuts the collagen into its component peptide chains. A mass spectrometer uses a laser to impart an electric charge to the peptides, which then race toward a detector that measures when each peptide strikes it. The resulting spectrum of values is a distinctive "fingerprint" that can be compared with a library of collagen fingerprints of known species to identify a mystery bone.

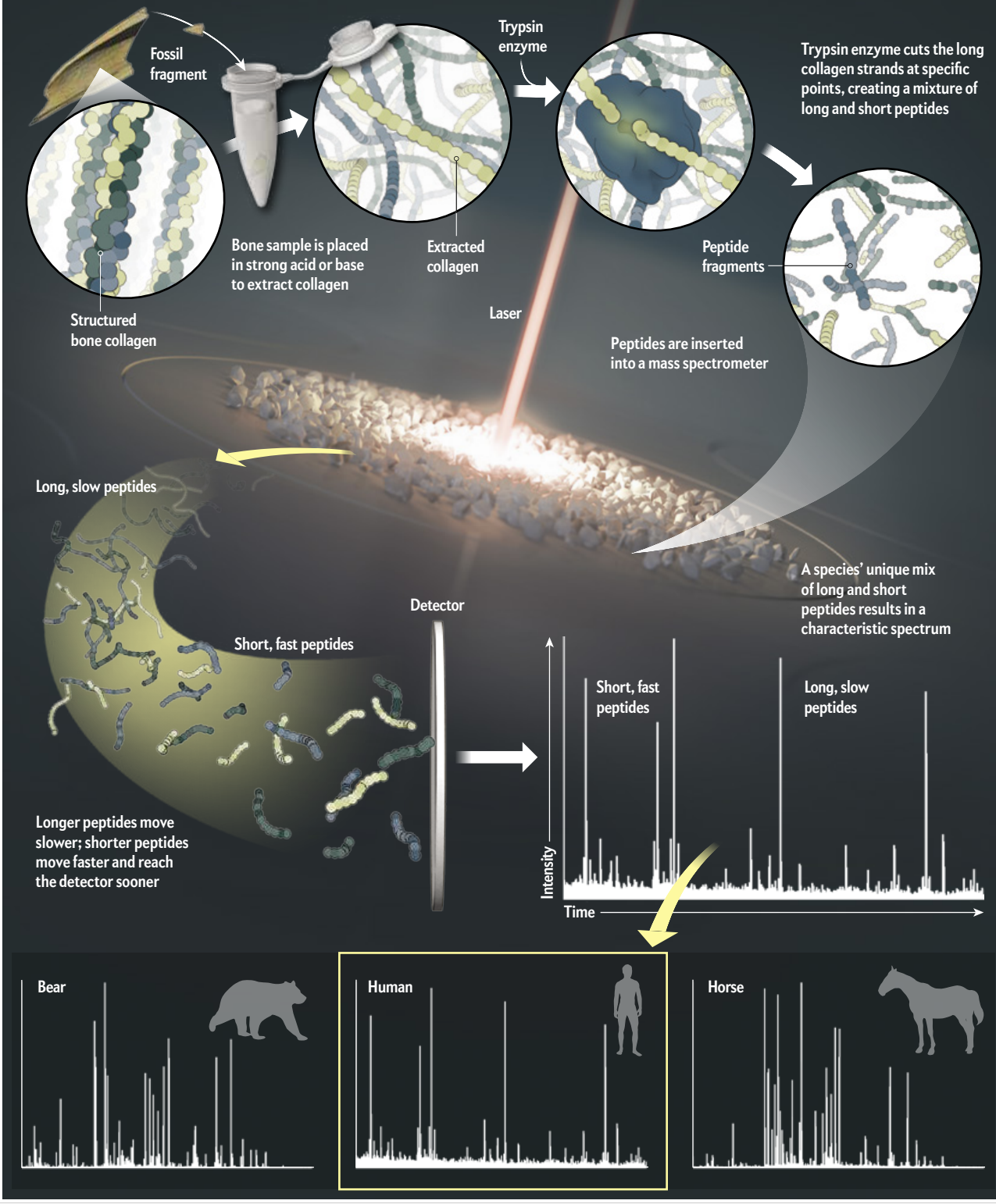
Fossil fragment
Structured bone collagen
Bone sample is placed in strong acid or base to extract collagen
Extracted collagen
Trypsin enzyme
Trypsin enzyme cuts the long collagen strands at specific points, creating a mixture of long and short peptides
Peptide fragments
Laser
Peptides are inserted into a mass spectrometer
Long, slow peptides
Short, fast peptides
Detector
Longer peptides move slower; shorter peptides move faster and reach the detector sooner
A species' unique mix of long and short peptides results in a characteristic spectrum
Short, fast peptides
Long, slow peptides
Intensity
Time
Bear
Human
Horse

Illustration by Falconieri Visuals

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centimeters long. The X woman finger bone, for instance, was about the size of a lentil and weighed less than 40 milligrams. A great proportion of bone material at the site was broken, principally because of the activity of predators such as hyenas, which den in caves to have their young and chew up bones while feeding. Since 2008 more than 135,000 bones have been excavated at Denisova, but 95 percent of them cannot be identified taxonomically, because they are too fragmentary. In contrast, the preservation of biomolecules in these fragments—including those molecules that make up DNA—is amazing: the two most complete ancient hominin genomes ever recovered come from Denisova fossils. What if, we wondered, there were a way of screening these many thousands of bone fragments at the site to find more human bones? If we could do this, perhaps we could generate more genetic and chronometric data or even find a new type of hominin lurking in the cave. It was then that we realized that we might be able to carry out exactly this kind of screening using ZooMS.

ZooMS, also called collagen peptide mass fingerprinting, allows investigators to assign fragments of bone to the proper taxonomic group by analyzing the proteins in bones. Bone collagen protein is made up of hundreds of small compounds called peptides that vary slightly among different types of animals. By comparing the peptide signatures of mystery bones against a library of such signatures from known animals, it is possible to assign the unidentified bones to the correct family, genus and sometimes species. First developed by Michael Buckley, now at the University of Manchester, and Matthew Collins of the University of York, both in England, ZooMS has been employed for more than a decade to identify the animal bones at archaeological sites. It is relatively cheap, costing around $5 to $10 per sample, and minimally destructive—it requires only around 10 to 20 milligrams of bone for analysis. It is also rapid; one person can screen hundreds of bones a week.

To our knowledge, no one had used ZooMS to search for human bones before. But we figured we had a shot. Even small fragments should be potentially useful, we reasoned, because the bone collagen and DNA preservation in Denisova is unsurpassed, given its stable and very low average annual temperature of below zero degrees Celsius. We knew we would not be able to get species-level identification with ZooMS. The collagen peptide signatures of human species and the great apes are too similar to discriminate. But no great apes are known to have roamed this part of the world during the Paleolithic. So if we could identify a piece of bone as belonging to a member of the group that comprises great apes and humans—together known as Hominidae—we could be fairly certain that it belonged to a human of some kind and subject it to genetic analysis that could provide the species identification.

Ancient DNA expert Svante Pääbo of the Max Planck Institute for Evolutionary Anthropology, who leads the Neandertal Genome Project and whose group published the Denisovan genome in 2010, was at Denisova for the 2014 meeting. We had not formally met Pääbo before, and we were keen to see what he thought of our idea for screening bone fragments and whether he would be interested in collaborating on that effort. He jumped at the chance and gave his immediate support. We then discussed our plan with Anatoly Derevianko of the Russian Academy of Sciences, who oversees work done at Denisova, and Michael Shunkov, director of the excavations. Both were interested. And so later that year we began the process of sampling a few thousand little fragments of, for all intents and purposes, "worthless" bones that had been recently excavated from the site.

In the abstract, it seemed like it would be quick work. In reality, we were faced with the massive job of painstakingly removing a minuscule sample of bone from each fragment for analysis, taking care not to touch the potentially valuable specimens with anything that might contaminate them. One of our students, Samantha Brown, who took on the project for her master's research dissertation, carried out much of this work, logging countless hours at our lab at the University of Oxford.

What we had found was not a Neandertal but an individual with a Neandertal mother and a Denisovan father.

Buckley collaborated with us on this project. Once we had 700 to 800 bone samples ready, Brown went to his lab to prepare and analyze them. The results were interesting: we had mammoths, hyenas, horses, reindeer, woolly rhinos—the full panoply of Ice Age beasts—but sadly, none of the peptide signatures corresponded with Hominidae. It was disappointing, but we decided to try a second batch to see whether we could locate even one human bone from the mass of fragments. Although we did not fancy our chances, we were hoping to be proved wrong.

Then one evening in the summer of 2015 we received an e-mail from Buckley. He had noticed that one of our samples, DC1227, had the characteristic peptide markers coding for Hominidae. We had a fragment of human bone—the proverbial needle in the haystack! We were ecstatic; our crazy idea seemed to have actually panned out.

Early the next day we went to our lab at Oxford to find the bone among the archived samples. We were somewhat deflated when we saw that the bone we had found was tiny even for a Denisova specimen—only 25 millimeters long—which did not leave much for further studies. But given the exceptional biomolecular preservation of the Denisova remains, we believed that it

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ANALYZING fossil fragments using ZooMS requires sawing off a 20-milligram sample from each tiny specimen (*1*). Other samples are prepared for radiocarbon dating (*2*).

would be enough to allow us to apply the techniques we wanted to use to find out as much about the bone as possible. We photographed it at high resolution, put it through a CT scanner, and drilled additional samples for dating and isotope analysis before Brown took the bone to Leipzig for DNA analysis in Pääbo's lab.

Several weeks later the dating results came back. The absence of any traceable radioactive carbon in the sample implied that our little bone was more than 50,000 years old. And before long, we learned from Pääbo that its mitochondrial DNA—which resides in the energy-producing organelles of cells and is passed down from mother to child—indicated that the bone came from an individual who had a Neandertal mother. We had found a hominin bone fragment hidden among thousands of "junk" bones and proved that the concept could work. Pääbo's team was planning to extract the much more informative nuclear genome from the bone, which now went by the site fossil I.D. "Denisova 11," or "Denny," as we nicknamed it. In the meantime, we decided to test our approach at another site.

US VS. THEM

VINDIJA CAVE in Croatia is a key site for understanding late Neandertals in Europe. For many years radiocarbon dates indicated that Neandertals there might have survived until 30,000 years ago, providing evidence for a potential overlap phase with anatomically modern humans, who arrived in the region by 42,000 to 45,000 years ago. Such a lengthy coexistence hinted that rather than being driven to extinction by modern humans, the Neandertals had been assimilated into their population. While reassessing the Vindija chronology, we decided it might be interesting to use ZooMS to assess the unidentified bones from the site. Previous work on the more complete bones from Vindija had shown that cave bears dominate the remains, accounting for some 80 percent of the bones, so we were not expecting to find the variety and breadth of fauna that we had detected at Denisova. Cara Kubiak, then another of our students, took on the project.

Surprisingly, the 28th sample out of the 383 we analyzed yielded a peptide sequence consistent with Hominidae. Later, Pääbo's team confirmed it genetically as a Neandertal. This bone was around seven centimeters long and, intriguingly, exhibited cut marks and other signs of human modification. Neandertal bones sometimes bear these markings, which may well be evidence of butchery and cannibalism.

The specimen, known as Vi-*28, turned out to be pivotal for our chronology work. Historically, archaeologists and preparators treated the bones from Vindija with conservation products to protect them. That practice makes radiocarbon dating very difficult because these products add carbon to the bone. Unlike other human bones from the site, Vi-*28 was not conserved; misidentified as an animal bone, it had eluded treatment—a boon for us. Radiocarbon dating of Vi-*28

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revealed that it belonged to a Neandertal from more than 47,000 years ago. This finding, published in 2017, along with dates we obtained from other Neandertals, showed that they disappeared from Vindija more than 40,000 years ago, before modern humans arrived at the site. The earlier dating results suggesting that they had persisted until at least 30,000 years ago were a fiction, influenced by contaminating carbon that had not been effectively removed. ZooMS again had proved its worth.

Other teams have had great success with the technique, too. In 2016 Frido Welker, now at the Natural History Museum of Denmark, and his colleagues reported that they had used ZooMS to identify 28 previously unrecognized hominin fossils among the unidentified bone fragments from the famed site of Grotte du Renne in the Burgundy region of France. Decades ago researchers working there found Neandertal bones in association with an array of surprisingly sophisticated artifacts, including bone tools, as well as pendants and other body ornaments—elements of a so-called Châtelperronian culture that is said to be transitional between the Middle Paleolithic and the Upper Paleolithic. The discovery ran counter to the long-held idea that *H. sapiens* alone was capable of such ingenuity. In so doing, it touched off an enduring debate over whether the Neandertals were truly associated with the advanced artifacts or whether the archaeological levels at the site had been disturbed somehow, mixing Neandertal bones with later artifacts left behind by *H. sapiens*.

The 28 bone fragments Welker and his colleagues identified as human using ZooMS all clearly came from the same layer as the advanced tools and ornaments. When they had the bones sequenced, the results were unequivocal: the specimens were Neandertal, not *H. sapiens*. The work lends considerable support to the notion that Neandertals did indeed make the Châtelperronian and other transitional industries and that they were cleverer than they have often been given credit for.

A HYBRID CHILD

THROUGHOUT OUR WORK at Vindija, we continued to analyze samples from Denisova in the hope that we could add more human fossils to our collection. Our efforts yielded two more Hominidae hits: DC3573, which turned out to belong to a Neandertal from more than 50,000 years ago, and DC3758, a 46,000-year-old bone that unfortunately does not preserve any ancient DNA. More than 5,000 bone fragments have now given us a total of five hominin bones that might have languished in obscurity forever if not for ZooMS.

But the most exciting development was yet to come. In May 2017 we were at the Max Planck Institute for Evolutionary Anthropology and met with senior members of Pääbo's lab, including Matthias Meyer and Janet Kelso. We wanted to know about the status of Denisova 11 and whether they had managed to retrieve nuclear DNA, which would give us a much more detailed picture of who Denisova 11 was.

It is not often in science that one receives completely jaw-dropping news, but Meyer and Kelso delivered exactly that. The nuclear DNA, they said, was curiously split: half was consistent with a Neandertal, and the other half appeared to be derived from a Denisovan. They thought Denisova 11 was a 50–50 hybrid. To exclude all possibility of error, the team was running the samples again to verify this astonishing result. Several months later the final data confirmed this initial finding. The mitochondrial DNA had given us only half of the picture. What we had found was not a Neandertal but an individual with a Neandertal mother and a Denisovan father—a first-generation hybrid, in the parlance of geneticists. The Denisova team announced this astounding discovery in the September 6, 2018, *Nature*, in a paper led by Viviane Slon of the Max Planck Institute for Evolutionary Anthropology.

We know now from the DNA that Denisova 11 was a female who probably lived around 90,000 to 100,000 years ago. And bone-density analysis generated from the CT scan we performed allowed our colleague Bence Viola of the University of Toronto to tentatively estimate her age at death at a minimum of 13 years old. Her Denisovan father himself had a distant Neandertal relative several hundred generations back. Of course, we can never know how these unions came about in prehistory, only that they did. Neither can we establish how Denisova 11 died, just that her remains were probably deposited in the cave sediment by a predator, possibly a hyena.

We will never know whether she died and was ceremonially buried by her loved ones, only to be scavenged by the hyena later, or lost her life to a predator. For tens of millennia this minute piece of her body lay undisturbed in the cave and might well have remained there for many more years, had it not been for the cutting-edge science that has allowed us to breathe life into her story. We are hopeful that ZooMS will help us unlock many more such secrets archived in bone. SA

Thomas Higham is director of the Oxford Radiocarbon Accelerator Unit at the University of Oxford. His research focuses on the dating of bone at archaeological sites in Eurasia spanning the Middle and Upper Paleolithic periods.

Katerina Douka is an archaeological scientist at the Max Planck Institute for the Science of Human History in Jena, Germany. She is leading a team to discover fossils of Neandertals and Denisovans among collections of unidentified bone fragments from sites in Asia.

MORE TO EXPLORE

Identification of a New Hominin Bone from Denisova Cave, Siberia Using Collagen Fingerprinting and Mitochondrial DNA Analysis. Samantha Brown et al. in *Scientific Reports*, Vol. 6, Article No. 23559; March 29, 2016.

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AN EVOLVED UNIQUENESS

How we became a different kind of animal

By Kevin Laland

Illustration by Victo Ngai

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MOST PEOPLE ON THIS PLANET BLITHELY ASSUME, LARGELY without any valid scientific rationale, that humans are special creatures, distinct from other animals. Curiously, the scientists best qualified to evaluate this claim have often appeared reticent to acknowledge the uniqueness of *Homo sapiens,* perhaps for fear of reinforcing the idea of human exceptionalism put forward in religious doctrines. Yet hard scientific data have been amassed across fields ranging from ecology to cognitive psychology affirming that humans truly *are* a remarkable species.

IN BRIEF

Human accomplishments derive from our ability to acquire knowledge from others and to use that communal store of experience to devise novel solutions to life's challenges.
Other species innovate, too. Chimps open nuts with stone hammers. Dolphins use a tool to flush out hidden prey.
Our uniqueness has to do with a capacity to teach skills to others over the generations with enough precision for building skyscrapers or going to the moon.

The density of human populations far exceeds what would be typical for an animal of our size. We live across an extraordinary geographical range and control unprecedented flows of energy and matter: our global impact is beyond question. When one also considers our intelligence, powers of communication, capacity for knowledge acquisition and sharing—along with magnificent works of art, architecture and music we create—humans genuinely do stand out as a very different kind of animal. Our culture seems to separate us from the rest of nature, and yet that culture, too, must be a product of evolution.

The challenge of providing a satisfactory scientific explanation for the evolution of our species' cognitive abilities and their expression in our culture is what I call "Darwin's Unfinished Symphony." That is because Charles Darwin began the investigation of these topics some 150 years ago, but as he himself confessed, his understanding of how we evolved these attributes was in his own words "imperfect" and "fragmentary." Fortunately, other scientists have taken up the baton, and there is an increasing feeling among those of us who conduct research in this field that we are closing in on an answer.

The emerging consensus is that humanity's accomplishments derive from an ability to acquire knowledge and skills from other people. Individuals then build iteratively on that reservoir of pooled knowledge over long periods. This communal store of experience enables creation of ever more efficient and diverse solutions to life's challenges. It was not our large brains, intelligence or language that gave us culture but rather our culture that gave us large brains, intelligence and language. For our species and perhaps a small number of other species, too, culture transformed the evolutionary process.

The term "culture" implies fashion or haute cuisine, but boiled down to its scientific essence, culture comprises behavior patterns shared by members of a community that rely on socially transmitted information. Whether we consider automobile designs, popular music styles, scientific theories or the foraging of small-scale societies, all evolve through endless rounds of innovations that add incremental refinements to an initial baseline of knowledge. Perpetual, relentless copying and innovation—that is the secret of our species' success.

ANIMAL TALENTS

COMPARING HUMANS with other animals allows scientists to determine the ways in which we excel, the qualities we share with other species and when particular traits evolved. A first step to understanding how humans got to be so different, then, is to take this comparative perspective and investigate the social learning and innovation of other creatures, a search that leads ultimately to the subtle but critical differences that make us unique.

Many animals copy the behavior of other individuals and in this way learn about diet, feeding techniques, predator avoidance, or calls and songs. The distinctive tool-using traditions of different populations of chimpanzees throughout Africa are a famous example. In each community, youngsters

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FOLLOWING in the steps of others—social learning—has been a key to the success of *Homo sapiens* as long as it has existed as a separate species. Here members of the San group in Namibia walk the dunes single file.

learn the local behavior—be it cracking open nuts with a stone hammer or fishing for ants with a stick—by copying more experienced individuals. But social learning is not restricted to primates, large-brained animals or even vertebrates. Thousands of experimental studies have demonstrated copying of behavior in hundreds of species of mammals, birds, fishes and insects. Experiments even show that young female fruit flies select as mates males that older females have chosen.

A diverse range of behaviors are learned socially. Dolphins possess traditions for foraging using sea sponges to flush out fish hiding on the ocean floor. Killer whales have seal-hunting traditions, including the practice of knocking seals off ice floes by charging toward them in unison and creating a giant wave. Even chickens acquire cannibalistic tendencies through social learning from other chickens. Most of the knowledge transmitted through animal populations concerns food—what to eat and where to find it—but there are also extraordinary social conventions. One troop of capuchin monkeys in Costa Rica has devised the bizarre habit of inserting fingers into the eye sockets or nostrils of other monkeys or hands into their mouths, sitting together in this manner for long periods and gently swaying—conventions that are thought to test the strength of social bonds.

Animals also "innovate." When prompted to name an innovation, we might think of the invention of penicillin by Alexander Fleming or the construction of the World Wide Web by Tim Berners-Lee. The animal equivalents are no less fascinating. My favorite concerns a young chimpanzee called Mike, whom primatologist Jane Goodall observed devising a noisy dominance display that involved banging two empty kerosene cans together. This exhibition thoroughly intimidated Mike's rivals and led to him shooting up the social rankings to become alpha male in record time. Then there is the invention by Japanese carrion crows of using cars to crack open nuts. Walnut shells are too tough for crows to crack in their beaks, but they nonetheless feed on these nuts by placing them in the road for cars to run over, returning to retrieve their treats when the lights turn red. And a group of starlings—birds famously fond of shiny objects used as nest decorations—started raiding a coin machine at a car wash in Fredericksburg, Va., and made off with, quite literally, hundreds of dollars in quarters.

Such stories are more than just enchanting snippets of natural history. Comparative analyses reveal intriguing patterns in the social learning and innovation exhibited by animals. The most significant of these discoveries finds that innovative species, as well as animals most reliant on copying, possess unusually large brains (both in absolute terms and relative to body size). The correlation between rates of innovation and brain size was initially observed in birds, but this research has since been replicated in primates. These findings support a hypothesis known as cultural drive, first proposed by University of California, Berkeley, biochemist Allan C. Wilson in the 1980s.

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Wilson argued that the ability to solve problems or to copy the innovations of others would give individuals an edge in the struggle to survive. Assuming these abilities had some basis in neurobiology, they would generate natural selection favoring ever larger brains—a runaway process culminating in the huge organs that orchestrate humans' unbounded creativity and all-encompassing culture.

Initially scientists were skeptical of Wilson's argument. If fruit flies, with their tiny brains, could copy perfectly well, then why should selection for more and more copying generate the proportionately gigantic brains seen in primates? This conundrum endured for years, until an answer arose from an unexpected source.

COPYCATS

THE SOCIAL LEARNING STRATEGIES TOURNAMENT was a competition that my colleagues and I organized that was designed to work out the best way to learn in a complex, changing environment. We envisaged a hypothetical world in which individuals—or agents as they are called—could perform a large number of possible behaviors, each with its own characteristic payoff that changed over time. The challenge was to work out which actions would give the best returns and to track how these changed. Individuals could either learn a new behavior or perform a previously learned one, and learning could occur through trial-and-error or through copying other individuals. Rather than trying to solve the puzzle ourselves, we described the problem and specified a set of rules, inviting anyone interested to have a go at solving it. All the entries—submitted as software code that specified how the agents should behave—competed against one another in a computer simulation, and the best performer won a €10,000 prize. The results were highly instructive. We found a strong positive relation between how well an entry performed and how well it required agents to learn socially. The winning entry did not require agents to learn often, but when they did, it was almost always through copying, which was always performed accurately and efficiently.

Brains are energetically costly organs, and social learning is paramount to animals that need to gather the resources necessary to grow and maintain a large brain efficiently.

The tournament taught us how to interpret the positive relation between social learning and brain size observed in primates. The results suggested that natural selection does not favor more and more social learning but rather a tendency toward better and better social learning. Animals do not need a big brain to copy, but they do need a big brain to copy well.

This insight stimulated research into the empirical basis of the cultural drive hypothesis. It led to the expectation that natural selection ought to favor anatomical structures or functional capabilities in the primate brain that promote accurate, efficient copying. Examples might include better visual perception if that allows copying over greater distances or imitating fine-motor actions. In addition, selection should foster greater connections between perceptual and motor structures in the brain, helping individuals to translate the sight of others performing a skill into their producing a matching performance by moving their body in a corresponding way.

The same cultural drive hypothesis also predicted that selection for improved social learning should have influenced other aspects of social behavior and life history, including living in social groups and using tools. The reasoning was that the bigger the group and the more time spent in the company of others, the greater the opportunities for effective social learning. Through copying, monkeys and apes acquire diverse foraging skills ranging from extractive foraging methods such as digging grubs out of bark to sophisticated tool-using techniques such as fishing for termites with sticks.

If social learning is what allows primates to pick up difficult-to-learn but productive food-procurement methods, any species proficient in social learning should show elevated levels of extractive foraging and tool use. They should possess a richer diet and have longer lives, if that gives more time for learning new skills and passing them on to descendants. In sum, cultural drive predicts that rates of social learning will correlate not only with brain size but also with a host of measures related to cognitive performance.

Rigorous comparative analyses have borne out these predictions. Those primates that excel at social learning and innovation are the same species that have the most diverse diets, use tools and extractive foraging, and exhibit the most complex social behavior. In fact, statistical analyses suggest that these abilities vary in lockstep so tightly that one can align primates along a single dimension of general cognitive performance, which we call primate intelligence (loosely analogous to IQ in humans).

Chimpanzees and orangutans excel in all these performance measures and have high primate intelligence, whereas some nocturnal prosimians are poor at most of them and have a lower metric. The strong correlations between primate intelligence and both brain size measures and performance in

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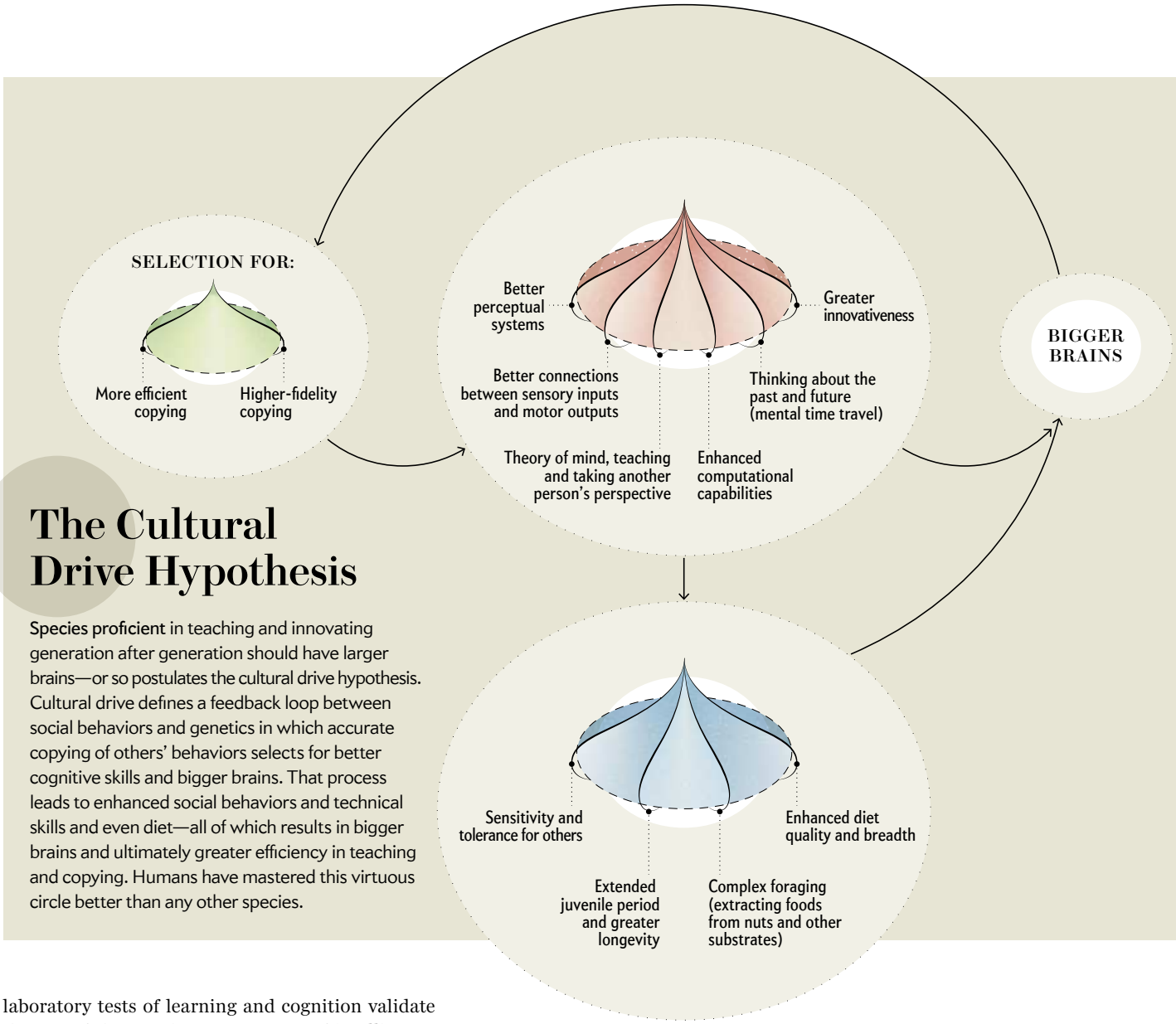
SELECTION FOR:
More efficient copying
Higher-fidelity copying
Better perceptual systems
Greater innovativeness
Better connections between sensory inputs and motor outputs
Thinking about the past and future (mental time travel)
Theory of mind, teaching and taking another person's perspective
Enhanced computational capabilities
BIGGER BRAINS
Sensitivity and tolerance for others
Enhanced diet quality and breadth
Extended juvenile period and greater longevity
Complex foraging (extracting foods from nuts and other substrates)

The Cultural Drive Hypothesis

Species proficient in teaching and innovating generation after generation should have larger brains—or so postulates the cultural drive hypothesis. Cultural drive defines a feedback loop between social behaviors and genetics in which accurate copying of others' behaviors selects for better cognitive skills and bigger brains. That process leads to enhanced social behaviors and technical skills and even diet—all of which results in bigger brains and ultimately greater efficiency in teaching and copying. Humans have mastered this virtuous circle better than any other species.

laboratory tests of learning and cognition validate the use of the metric as a measure of intelligence. The interpretation also fits with neuroscientific analyses showing that the size of individual brain components can be accurately predicted with knowledge of overall brain size. Associated with the evolution of large primate brains are bigger and better-connected regions—neocortices and cerebellums—that allow executive control of actions and increased cortical projections to the motor neurons of the limbs, facilitating controlled and precise movements. This helps us to understand why big-brained animals show complex cognition and tool use. [For more on primate brains, see "Are We Wired Differently?" on page 70.]

Plotting the intelligence measure on a primate family tree reveals evolution for higher intelligence taking place independently in four distinct primate groups: the capuchins, macaques, baboons and great apes—precisely those species renowned for their social learning and traditions. This finding is exactly the pattern expected if cultural processes really were driving the evolution of brain and cognition. Further analyses, using better data and cutting-edge statistical methods, reinforce these conclusions, as do models that make quantitative predictions for brain and body size based on estimates of the brain's metabolic costs.

Cultural drive is not the only cause of primate brain evolution: diet and sociality are also important because fruit-eating primates and those living in large, complex groups possess large brains. It is difficult, however, to escape the conclusion that high intelligence and longer lives co-evolved in some primates because their cultural capabilities allowed them to exploit high-quality but difficult-to-access food resources, with the nutrients gleaned "paying" for brain growth. Brains are energetically costly organs, and social learning is paramount to animals gathering the resources necessary to grow and maintain a large brain efficiently.

Graphic by Federica Fragapane

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NO CHIMP MOBILES

WHY, THEN, DON'T OTHER PRIMATES have complex culture like us? Why haven't chimpanzees sequenced genomes or built space rockets? Mathematical theory has provided some answers. The secret comes down to the fidelity of information transmission from one member of a species to another, the accuracy with which learned information passes between transmitter and receiver. The size of a species' cultural repertoire and how long cultural traits persist in a population both increase exponentially with transmission fidelity. Above a certain threshold, culture begins to ratchet up in complexity and diversity. Without accurate transmission, cumulative culture is impossible. But once a given threshold has been surpassed, even modest amounts of novel invention and refinement can lead rapidly to massive cultural change. Humans are the only living species to have passed this threshold.

Our ancestors achieved high-fidelity transmission through teaching—behavior that functions to facilitate a pupil's learning. Whereas copying is widespread in nature, teaching is rare, and yet teaching is universal in human societies once the many subtle forms this practice takes are recognized. Mathematical analyses reveal tough conditions that must be met for teaching to evolve, but they show that cumulative culture relaxes these conditions. The modeling implies that teaching and cumulative culture coevolved in our ancestors, creating for the first time in the history of life on our planet a species whose members taught their relatives a broad range of skills, perhaps cemented through goal-oriented "deliberate" practice.

The teaching of cultural knowledge by hominins (humans and their extinct close relatives) included foraging, food processing, learned calls, toolmaking, and so forth and provided the context in which language first appeared. Why our ancestors alone evolved language is one of the great unresolved questions. One possibility is that language developed to reduce the costs, increase the accuracy and expand the domains of teaching. Human language may be unique, at least among extant species, because only humans constructed a sufficiently diverse and dynamic cultural world that demanded talking about. This explanation has the advantage that it accounts for many of the characteristic properties of language, including its distinctiveness, its power of generalization and why it is learned [see "Talking through Time," on page 64].

Language began as just a handful of shared symbols. But once started, the use of protolanguage imposed selection on hominin brains for language-learning skills and on languages themselves to favor easy-to-learn structures. That our ancestors' cultural activities imposed selection on their bodies and minds—a process known as gene culture co-evolution—is now well supported. Theoretical, anthropological and genomic analyses all demonstrate how socially transmitted knowledge, including that expressed in the manufacture and use of tools, generated natural selection that transformed human anatomy and cognition. This evolutionary feedback shaped the emergence of the modern human mind, generating an evolved psychology that spurred a motivation to teach, speak, imitate, emulate, and share the goals and intentions of others. It also produced enhanced learning and computational abilities. These capabilities evolved with cumulative culture because they enhance the fidelity of information transmission.

Teaching and language were evolutionary game changers for our lineage. Large-scale cooperation arose in human societies because of our uniquely potent capacities for social learning and teaching, as theoretical and experimental data attest. Culture

CHIMPS AND HUMANS are toolmakers. Chimpanzees (*1*) use sticks to hunt for a meal of termites and pass this technique along to their kin. Unlike chimps, humans (*2*) transmit cultural knowledge to offspring with a high degree of precision that enables the making of sophisticated technologies.

1

2

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took human populations down novel evolutionary pathways, both by creating conditions that promoted established mechanisms for cooperation witnessed in other animals (such as helping those that reciprocate) and by generating novel cooperative mechanisms not seen elsewhere. Cultural group selection—practices that help a group cooperate and compete with other groups (forming an army or building an irrigation system)—spread as they proved their worth [see "The Origins of Morality," on page 74].

Culture provided our ancestors with food-procurement and survival tricks, and as each new invention arose, a given population was able to exploit its environment more efficiently. This occurrence fueled not only brain expansion but population growth as well. Increases in both human numbers and societal complexity followed our domestication of plants and animals. Agriculture freed societies from the constraints that the peripatetic lives of hunter-gatherers imposed on population size and any inclinations to create new technologies. In the absence of this constraint, agricultural societies flourished, both because they outgrew hunter-gatherer communities through allowing an increase in the carrying capacity of a particular area for food production and because agriculture triggered a raft of associated innovations that dramatically changed human society. In the larger societies supported by increasing farming yields, beneficial innovations were more likely to spread and be retained. Agriculture precipitated a revolution not only by triggering the invention of related technologies—ploughs or irrigation technology, among others—but also by spawning entirely unanticipated initiatives, such as the wheel, city-states and religions.

The emerging picture of human cognitive evolution suggests that we are largely creatures of our own making. The distinctive features of humanity—our intelligence, creativity, language, as well as our ecological and demographic success—are either evolutionary adaptations to our ancestors' own cultural activities or direct consequences of those adaptations. For our species' evolution, cultural inheritance appears every bit as important as genetic inheritance.

We tend to think of evolution through natural selection as a process in which changes in the external environment, such as predators, climate or disease, trigger evolutionary refinements in an organism's traits. Yet the human mind did not evolve in this straightforward way. Rather our mental abilities arose through a convoluted, reciprocal process in which our ancestors constantly constructed niches (aspects of their physical and social environments) that fed back to impose selection on their bodies and minds, in endless cycles. Scientists can now comprehend the divergence of humans from other primates as reflecting the operation of a broad array of feedback mechanisms in the hominin lineage. Similar to a self-sustaining chemical reaction, a runaway process ensued that propelled human cognition and culture forward. Humanity's place in the evolutionary tree of life is beyond question. But our ability to think, learn, communicate and control our environment makes humanity genuinely different from all other animals. SA

A Visit from E.T.

Imagine an extraterrestrial intelligence studying Earth's biosphere. Which of all the species would it identify as differing from the rest? The answer is humanity. Here are a few reasons:

Population size. Our numbers are out of kilter with global patterns for vertebrate populations. There are several orders of magnitude more humans than expected for a mammal of our size.

Ecological range. Our species distribution is extraordinary. Humans have colonized virtually every region of the terrestrial globe.

Environmental regulation. Humans control vast and diverse flows of energy and matter on unprecedented scales.

Global impact. Human activities threaten and are driving extinct unmatched numbers of species while eliciting strong evolutionary change across the biosphere.

Cognition, communication and intelligence. Experiments demonstrate superior performance by humans across diverse tests of learning and cognition. Human language is infinitely flexible, unlike the communication of other animals.

Knowledge acquisition and sharing. Humans acquire, share and store information on never-before-seen scales and build on their pooled cultural knowledge cumulatively from generation to generation.

Technology. Humans invent and mass-produce infinitely more complex and diverse artifacts than other animals.

The extraterrestrials might well be charmed by the elephant's trunk and impressed by the giraffe's neck, but it is humans that they would single out. —*K.L.*

Kevin Laland is a professor of behavioral and evolutionary biology at the University of St. Andrews in Scotland and author of *Darwin's Unfinished Symphony: How Culture Made the Human Mind* (Princeton University Press, 2017).

MORE TO EXPLORE

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TALKING THROUGH TIME

What makes language distinctly human

By Christine Kenneally

Illustration by Victo Ngai

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DOLPHINS NAME ONE ANOTHER, AND THEY CLICK AND WHISTLE about their lives or the dangers posed by sharks and humans. They also pass on useful bits of know-how from mother to child, such as how to catch fish or how to flee. If they had language in the same sense that we do, however, they would not only pass down little bits of information but also aggregate them into a broad body of knowledge about the world. Over the span of generations clever practices, complex knowledge and technology based on two, three or several components would develop. Dolphins would have history—and with history, they would learn about the journeys and ideas of other dolphin groups, and any one individual could inherit a fragment of language, say, a story or poem, from another individual who had lived hundreds of years before. That dolphin would be touched, through language, by the wisdom of another dolphin, who was in every other way long gone.

IN BRIEF

Human communication is far more structured and complex than the gestures and sounds of other animals. **Scientists have failed,** however, to find distinctive physiological, neurological or genetic traits that could explain the uniqueness of human language. **Language appears instead** to arise from a platform of abilities, some of which are shared with other animals. **Intriguingly,** the intricacy of human language may arise from culture: the repeated transmission of speech through many generations.

Only humans can perform this spectacular time-traveling feat, just as only humans can penetrate the stratosphere or bake strawberry shortcake. Because we have language, we have modern technology, culture, art and scientific inquiry. We have the ability to ask questions such as, Why is language unique to humans? Despite the accumulated genius we inherit when we learn to speak or sign, we have yet to work out a good answer. But a diverse group of brain scientists, linguists, animal researchers and geneticists are tackling the question—so we are much closer to a real understanding than ever before.

AN UNANSWERABLE QUESTION

THAT LANGUAGE is uniquely human has been assumed for a long time. But trying to work out exactly how and why that is the case has been weirdly taboo. In the 1860s the Société de Linguistique de Paris banned discussion about the evolution of language, and the Philological Society of London banned it in the 1870s. They may have wanted to clamp down on unscientific speculation, or perhaps it was a political move—either way, more than a century's worth of nervousness about the subject followed. Noam Chomsky, the extraordinarily influential linguist at the Massachusetts Institute of Technology, was, for decades, rather famously disinterested in language evolution, and his attitude had a chilling effect on the field. Attending an undergraduate linguistics class in Melbourne, Australia, in the early 1990s, I asked my lecturer how language evolved. I was told that linguists did not ask the question, because it was not really possible to answer it.

Luckily, just a few years later, scholars from different disciplines began to grapple with the question in earnest. The early days of serious research in language evolution unearthed a perplexing paradox: Language is plainly, obviously, uniquely human. It consists of wildly complicated interconnecting sets of rules for combining sounds and words and sentences to create meaning. If other animals had a system that was the same, we would likely recognize it. The problem is that after looking for a considerable amount of time and with a wide range of methodological approaches, we cannot seem to find anything unique in ourselves—either in the human genome or in the human brain—that explains language.

To be sure, we have found biological features that are both unique to humans and important for language. For example, humans are the only primates to have voluntary control of their larynx: it puts us at risk of choking, but it allows us to articulate speech. But the equipment that seems to be designed for language never fully explains its enormous complexity and utility.

It seems more and more that the paradox is not inherent in language but in how we look at it. For a long time we have been in love with the idea of a sudden, explosive transformation that changed mere apes into us. The idea of metamorphosis has gone hand in hand with a list of equally dramatic ideas. For example: that language is a wholly dis-

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crete trait that has little in common with other kinds of mental activity; that language is the evolutionary adaptation that changed everything; and that language is wired into humanity's DNA. We have looked for a critical biological event that brought complex language into existence around 50,000 years ago.

Findings from genetics, cognitive science and brain sciences are now converging in a different place. It looks like language is not a brilliant adaptation. Nor is it encoded in the human genome or the inevitable output of our superior human brains. Instead language grows out of a platform of abilities, some of which are very ancient and shared with other animals and only some of which are more modern.

TALKING TO THE ANIMALS

ANIMAL RESEARCHERS were the first to challenge the definition of language as a discretely human attribute. As comparative psychologist Heidi Lyn has pointed out, the only way we can truly determine what is unique to human language is to explore the capacities of other animals. Interestingly, almost every time researchers have proposed that humans can do something that other animals cannot because humans have language, studies have shown that some animals can do some of those things, at least some of the time.

Take gestures, for example. Some are individual, but many are common to our language community and even to all humans. It is clear that language evolved as part of a communication system in which gesture also plays a role. But landmark work has shown that chimpanzees gesture in meaningful ways, too. Michael Tomasello, now emeritus at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and his colleagues have shown that all species of great apes will wait until they have another ape's attention before they signal, and they repeat gestures that do not get the response they want. Chimpanzees slap the ground or clap their hands to get attention—and just as a belligerent human might raise a fist, they roll their arms over their head (normally a prelude to an attack) as a warning to rivals.

Even so, Tomasello's laboratory found that apes were very poor at understanding a human pointing gesture that conveyed information, such as, for example, the location of a hidden object. Does pointing—or rather the ability to fully understand it—represent a critical step in the evolution of language? The claim struck Lyn, who worked with bonobos that are now at the Ape Cognition and Conservation Initiative, as absurd. "My apes understood when I pointed to things all the time," she says. But when she set up pointing experiments with chimpanzees at the Yerkes National Primate Research Center at Emory University, she was surprised to find that the apes there did not understand her pointing well at all. Then she went back to the bonobos in her lab and tested them. All of them did.

GETTY IMAGES

ALEX, a celebrated African grey parrot, could recognize and name some 100 different objects, along with their color, texture and shape, as well as convey his desires and intentions by means of sentences such as "Wanna go back." Chimpanzees can also be taught to use human language.

The difference between the pointing apes and the nonpointing apes had nothing to do with biology, Lyn concluded. The bonobos had been taught to communicate with humans using simple visual symbols; the chimpanzees had not. "It's apes that haven't been around humans in the same way that can't follow pointing," she explains.

The fact that the bonobos were taught by humans has been used to dismiss their ability, according to Lyn, as if they were somehow tainted. Language research with parrots and dolphins and other animals has been discounted for the same reason. Lyn argues, however, that animals trained by humans provide valuable insights. If creatures with different brains and different bodies can learn some humanlike communicative skills, it means that language should not be defined as wholly human and disconnected from the rest of the animal world. Moreover, whereas language may be affected by biology, it is not necessarily determined by it. With the bonobos, it was culture, not biology, that made the critical difference.

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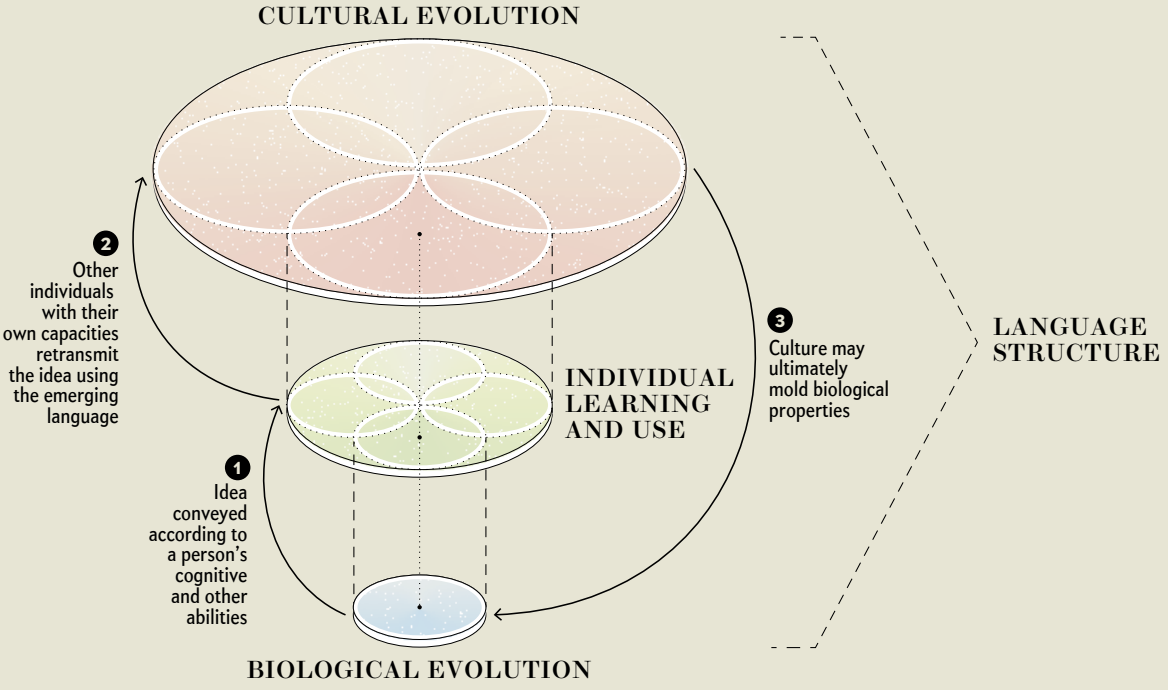
Evolution of Language

Languages have complex structures, which enable, say, English speakers to guess what "blue giraffe" might mean even if they have never before encountered that particular combination of words. Extensive studies by Simon Kirby of the University of Edinburgh and other linguists suggest that language structure derives from repeatedly using words to convey ideas through many generations. In a circular process repeated innumerable times, one speaker, or agent, passes a concept on to others ❶ via whatever string of words she or he has thus far learned. The ability to transmit an idea coherently depends on cognitive capacities inherited from parents. The recipients of this utterance understand it as best they can and convey it to others ❷ within the community, along with their own modifications. These changes accumulate over generations in the culture. Someone who can better master the emerging discourse of the community is assumed to be more likely to pass on his or her genes. Therefore, with time the accumulated cultural refinements may influence biological properties ❸. Amazingly, from this babel eventually emerges order, as the speakers, all trying to learn the language as best they can, converge on a single, structured language that is both learnable and useful for conveying information. In sum, language in all its complexity emerges from culture.


CULTURAL EVOLUTION
❷ Other individuals with their own capacities retransmit the idea using the emerging language
❸ Culture may ultimately mold biological properties
LANGUAGE STRUCTURE
INDIVIDUAL LEARNING AND USE
❶ Idea conveyed according to a person's cognitive and other abilities
BIOLOGICAL EVOLUTION

SOURCE: "CULTURE AND BIOLOGY IN THE ORIGINS OF LINGUISTIC STRUCTURE," BY SIMON KIRBY, IN *PSYCHONOMIC BULLETIN & REVIEW*, VOL. 24, NO. 1; FEBRUARY 2017

GENETIC CODE

THE LIST OF ABILITIES that were formerly thought to be a unique part of human language is actually quite long. It includes parts of language, such as words. Vervet monkeys use wordlike alarm calls to signal a specific kind of danger. Another crucial aspect is structure. Because we have syntax, we can produce an infinite number of novel sentences and meanings, and we can understand sentences that we have never heard before. Yet zebra finches have complicated structure in their songs, dolphins can understand differences in word order and even some monkeys in the wild seem to use one type of call to modify another. The list extends to types of cognition, such as theory of mind, which is the ability to infer others' mental states. Dolphins and chimpanzees are excellent at guessing what an interlocutor wants. Even the supposedly unique ability to think about numbers falls by the wayside—bees can understand the concept of zero, bees and rhesus monkeys can count to four, and cormorants used for fishing in China reportedly count to seven.

The list includes genes. The famous *FOXP2* gene, once called a language gene, is indeed a gene that affects language—when it is mutated, it disrupts articulation—but it performs other roles as well. There is no easy way to tease out the different effects. Genes are critical for understanding how language evolved, says Simon Fisher, a geneticist at the Max Planck Institute for Psycholinguistics in Nijmegen, the Netherlands, but "we have to think about what genes do." To put an incredibly complex process very briefly: genes code for proteins, which then affect cells, which may be brain cells that form neural circuits, and it is those circuits that are then responsible for behavior. "It may be that there is a network of genes that are important for syntactic processing or speaking proficiently," Fisher explains, "but there won't be a single gene that can magically code for a suite of abilities."

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The list of no-longer-completely-unique human traits includes brain mechanisms, too. We are learning that neural circuits can develop multiple uses. One recent study showed that some neural circuits that underlie language learning may also be used for remembering lists or acquiring complicated skills, such as learning how to drive. Sure enough, the animal versions of the same circuits are used to solve similar problems, such as, in rats, navigating a maze.

Michael Arbib, a cognitive neuroscientist at the University of California, San Diego, notes that humans have created "a material and mental world of ever increasing complexity"—and yet whether a child is born into a world with the steam train or one with the iPhone, he or she can master some part of it without alterations in biology. "As far as we know," Arbib says, "the only type of brain on earth that can do that is the human brain." He emphasizes, however, that the brain is just one part of a complex system, which includes the body: "If dolphins had hands, maybe they could have evolved that world."

Indeed, making sense of the human world requires not only the brain in the body but also a group of brains interacting as part of the human social world. Arbib refers to this as an EvoDevoSocio approach. Biological evolution influences the development and learning of individuals, and individual learning shapes the evolution of culture; learning, in turn, can be shaped by culture. To understand language, the human brain has to be considered a part of those systems. The evolution of language was polycausal, Arbib says. No one switch was thrown: there were lots of switches. And it did not happen all at once but took a great deal of time.

CULTURAL REVOLUTION

CULTURE ALSO PLAYS A CRITICAL ROLE for Simon Kirby, a cognitive scientist who runs the Center for Language Evolution at the University of Edinburgh. From the beginning, Kirby was fascinated by the idea that not only is language something that we learn from others, but it is something that is passed down through generations of learners. What impact did the repeated act of learning have on language itself?

Kirby set out to test the question by fashioning a completely new method of exploring language evolution. Instead of looking at animals or humans, he built digital models of speakers, called agents, and fed them messy, random strings of language. His artificially intelligent agents had to learn the language from other agents, but then they had to teach other agents the language as well. Then Kirby rolled over generations of learners and teachers to see how the language might change. He likened the task to the telephone game, where a message is passed on from one person to the next and so on, with the final message often ending up quite different from the original.

Kirby found that his digital agents had a tendency to produce more structure in their output than they had received in their input. Even though the strings of language he initially gave them were random, sometimes by chance a string might appear to be slightly ordered. Critically, the agents picked up on that structure, and they generalized it. "The learners, if you like, hallucinated structure in their input," Kirby says. Having seen structure where there was none, the agents then reproduced more structure in what they said.

The changes might be very tiny, Kirby notes, but over the generations "the process snowballs." Excitingly, not only did the agents' language begin to look more and more structured after many generations, the kind of structure that emerged looked like a simple version of that which occurs in natural human language. Subsequently Kirby tried a variety of different models and gave them different kinds of data, but he found that "the cumulative accretion of linguistic structure seemed to always happen no matter how we built the models." It was the crucible of learning over and over again that created the language itself.

Now Kirby is re-creating his digital experiments in real life with humans and even animals by getting them to repeat things that they learn. He is finding that structure indeed evolves in this way. One of the more thrilling implications of this discovery is how it helps to explain why we can never pin down the right single gene or mutation or brain circuit to explain language: it is just not there. Language seems to emerge out of a combination of biology, individual learning and the transmission of language from one individual to another. The three systems run at entirely different timescales, but when they interlock, something extraordinary happens: language is born.

In the short time since the field of language evolution has been active, researchers may have not reached the holy grail: a definitive event that explains language. But their work makes that quest somewhat beside the point. To be sure, language is probably the most unique biological trait on the planet. But it is much more fragile, fluky and contingent than anyone might have predicted. SA

Christine Kenneally is an award-winning science journalist and author of two books, most recently *The Invisible History of the Human Race* (Viking, 2014).

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ARE WE WIRED DIFFERENTLY?

Parts of the brain involved in language and cognition have enlarged greatly over an evolutionary timescale

By Chet C. Sherwood

Graphics by Mesa Schumacher

HUMANS ARE OFF THE SCALE. Modern human brains are about threefold larger than those of our earliest hominin ancestors and living great ape relatives. Across animals, brain size is tightly correlated with body size. But humans are the extreme outlier when gauged against this typical scaling relation. The average adult human brain is roughly three pounds, which is approximately 2 percent of body size. But it consumes an outsized 20 percent of the body's energy budget because of high levels of electrical activity by neurons and the metabolic fuel it takes to transmit chemical signals from one brain cell to the next.

Detailed comparisons of human brains with those of our close living primate relatives, including chimpanzees, have shown that the parts of the cerebral cortex involved in higher-order cognitive functions, such as creativity and abstract thinking, have become especially enlarged. These cortical areas, known as association regions, mature relatively late in postnatal development. Some of the long-range neural connections that link these association areas to one another and to the cerebellum (the latter plays a role in voluntary movement and learning new skills) are more numerous in human brains compared with other primates. These human-enhanced networks are loci for language, toolmaking and imitation. Even ancient reward systems in a subcortical area called the striatum, a hub of activity for the brain-signaling molecule dopamine, appear to have been reshaped in human brain evolution. That change most likely increases attention to social signals and facilitates language learning.

Where did our big brains come from? The hominin fossil record points to a general trend toward increased cranial capacity during the past six million years or so. That is when our lineage split from the last common ancestor we shared with chimpanzees and bonobos. Scientists consider a constellation of interrelated features of human biology to be associated with our large brains—slower growth through the stages of childhood, a longer life span, and more involvement in raising offspring by fathers and grandparents to assist mothers. Extended brain growth after birth means that significant events that lay the groundwork for cognition take place in a rich social and ecological context.

Another clue to what makes us different from chimpanzees and other intelligent species comes from compelling research that has uncovered genetic and molecular changes that occurred during the long course of the brain's evolution. A look at some of the distinctive features of the human brain follows.

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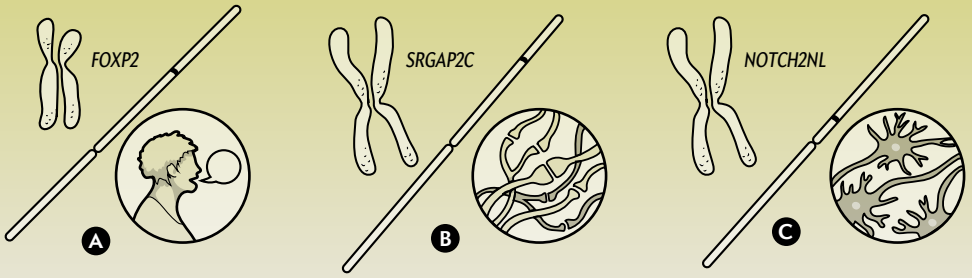
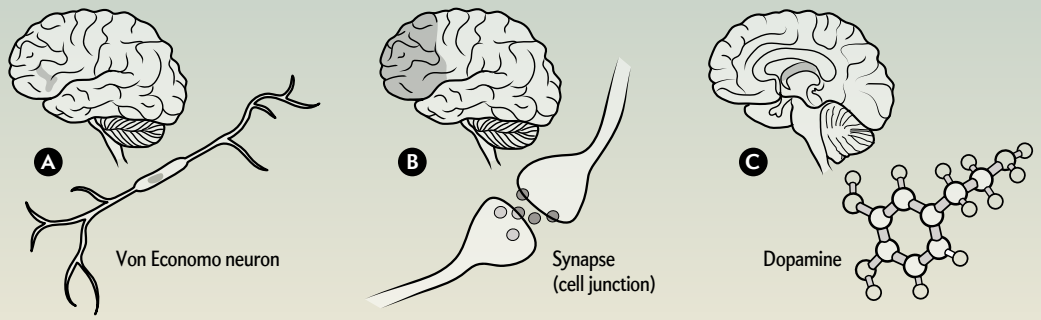


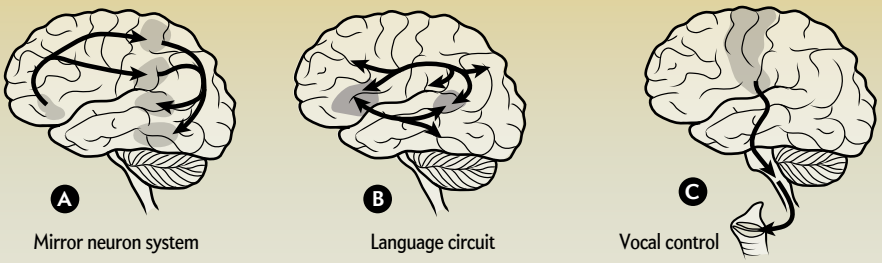
GENES

The variant of the *FOXP2* gene found in humans plays a role in vocal learning **A**. *SRGAP2C*, a unique duplicate of *SRGAP2* that is found only in humans, increases the density of neural connections **B**. A human version of a gene called *NOTCH*, known as *NOTCH2NL*, has three copies and aids in the production of neurons **C**.



CELLS

Von Economo neurons, which are pivotal in social-emotional brain circuits, are bigger in humans **A**. RNA that carries messages to instruct cells to make proteins is more active in the synapses of the prefrontal cortex (*dark area*) than it is in other primates **B**. Cells produce more of the neurotransmitter dopamine in the striatum. Dopamine is involved in various cognitive functions **C**.

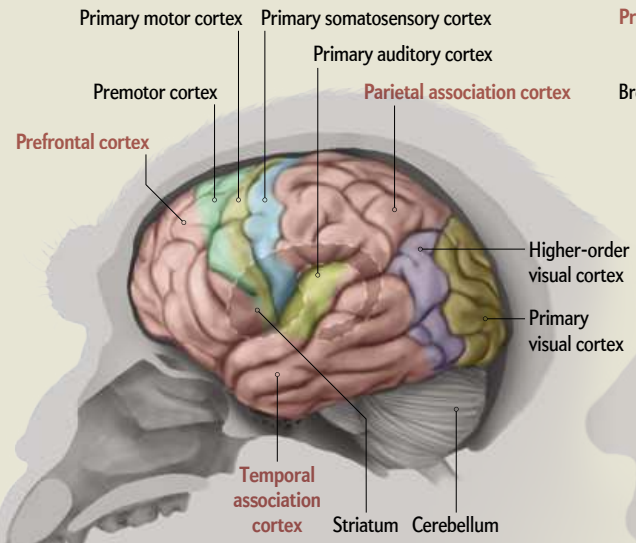


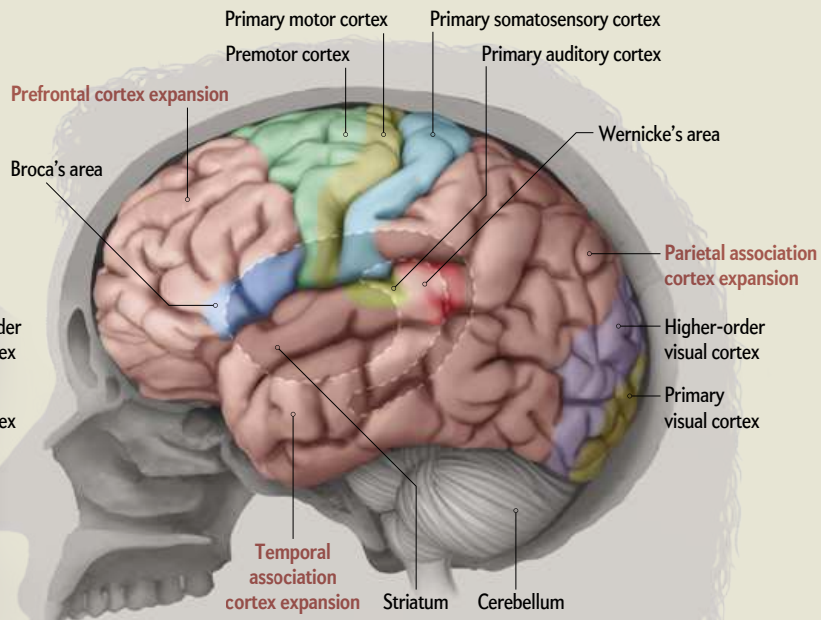
CIRCUITS

The mirror neuron system, activated when viewing the actions of others, has intricate circuitry in humans **A**. Expanded connections between two sites—Wernicke's and Broca's areas—form a vital circuit for language processing **B**. A link from the motor cortex to the brain stem coordinates the larynx muscles, a circuit absent in chimpanzees and macaques **C**.

REGIONAL EXPANSION

Brain areas responsible for higher cognitive functions grew disproportionately in humans compared with the same regions in chimpanzees—among them, the prefrontal, temporal association and parietal association cortices.





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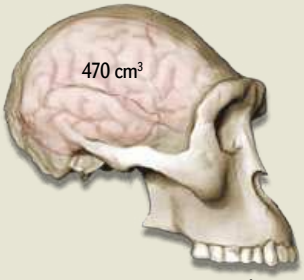
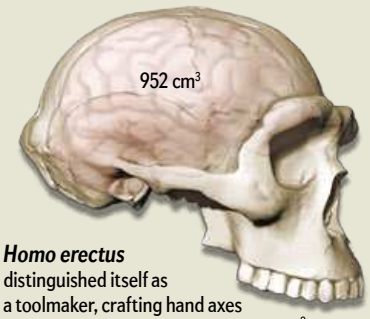
BIG BRAINS GOT US HERE

The last common ancestor that humans shared with chimpanzees and bonobos lived from six million to eight million years ago. After the two lines split, a number of evolutionary adaptations occurred: bipedalism, stone toolmaking and, notably, an increase in brain size in certain hominin species—a process that gained momentum as time passed.



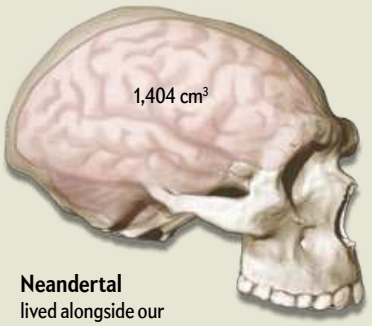
Australopithecus africanus
combined human and ape features. Its brain volume of 470 cubic centimeters (cm^3) was akin to that of chimpanzees.

3.3–2.1 million years ago (mya)



Homo erectus
distinguished itself as a toolmaker, crafting hand axes and expanding its home environment outside of Africa.

1.9 mya–143,000 years ago (143 kya)

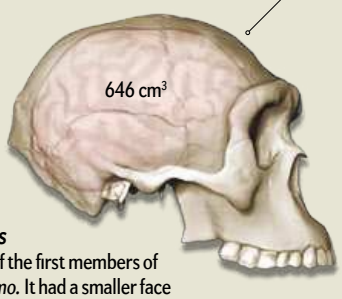


Neandertal
lived alongside our species and was an avid hunter and tool and fire user. Its braincase, at 1,404 cm^3, was comparable in volume to our own.

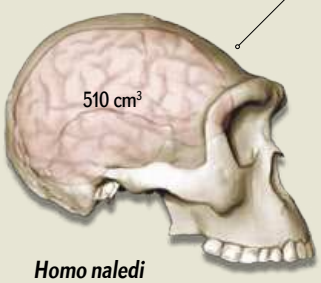
400–40 kya

335–236 kya

2.1–1.6 mya

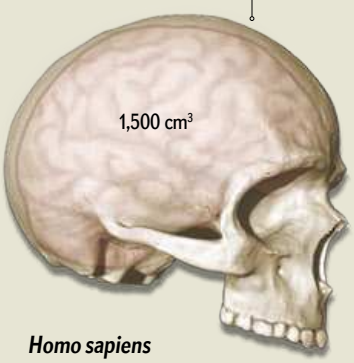


Homo habilis
became one of the first members of the genus *Homo*. It had a smaller face than its ancestors and developed frontal areas linked to language.



Homo naledi
was a newer member of the human lineage whose story demonstrates that evolution does not always move in straight lines. Its smaller braincase was 510 cm^3.

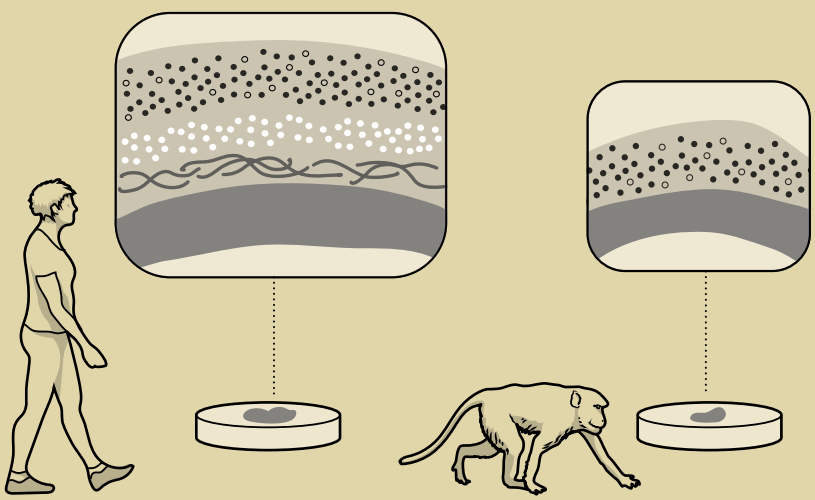
300 kya–present



Homo sapiens
evolved some 300,000 years ago. Our brain shape is spherical, or globular, because of the rounded shape of the parietal area and the cerebellum.

MINI BRAINS

Supplying nutrients to groups of stem cells in a lab dish allows them to grow into mini brains. These cerebral organoids, as they are called, consist of entire brain regions, such as the cortex of a human or a monkey (*cross-sectional views*). These ingenious research tools afford an opportunity to compare the activity of genes and neural circuit development in organoids with the working of actual brains in humans, nonhuman primates and other species, ultimately providing a clearer picture of what makes us unique.



HOW OUR BRAINS GROW

Compared with other primates, human babies have brains that are underdeveloped, grow more rapidly in the first year after birth, and then level off years later with a volume about three times larger than that of a chimpanzee.

SOURCES: "Developmental Patterns of Chimpanzee Cerebral Tissues Provide Important Clues for Understanding the Remarkable Enlargement of the Human Brain," by T. Sakai et al., in *Proceedings of the Royal Society B*, Vol. 270; February 22, 2013 (*brain area expansion*); "Mammalian Brains Are Made of These: A Dataset of the Numbers and Densities of Neuronal and Nonneuronal Cells in the Brain of Glires, Primates, Scandentia, Eulipotyphlans, Afrotherians and Artiodactyls, and Their Relationship with Body Mass," by S. Herculano-Houzel et al., in *Brain, Behavior and Evolution*, Vol. 86, Nos. 3–4; December 2015 (*human* and *macaque neuron numbers*); "Dogs Have the Most Neurons, though Not the Largest Brain: Trade-off between Body Mass and Number of Neurons in the Cerebral Cortex of Large Carnivoran Species," by D. Jardim-Messeder et al., in *Frontiers in Neuroanatomy*, Vol. 11, Article No. 118; December 2017 (*cat neuron number*); "Quantitative Relationships in Delphinid Neocortex," by H. S. Mortensen et al., in *Frontiers in Neuroanatomy*, Vol. 8, Article No. 132; November 2014 (*pilot whale neuron number*); "Cortical Cell and Neuron Density Estimates in One Chimpanzee Hemisphere," by C. E. Collins et al., in *PNAS*, Vol. 113, No. 3; January 19, 2016 (*chimpanzee neuron number*); "Human Evolutionary History," by E. K. Boyle and B. Wood, in *Evolution of Nervous Systems*. Second edition. Edited by J. H. Kaas. Academic Press, 2017 (*hominin evolution*); Smithsonian National Museum of Natural History *http://humanorigins.si.edu* (*hominin species time line*)

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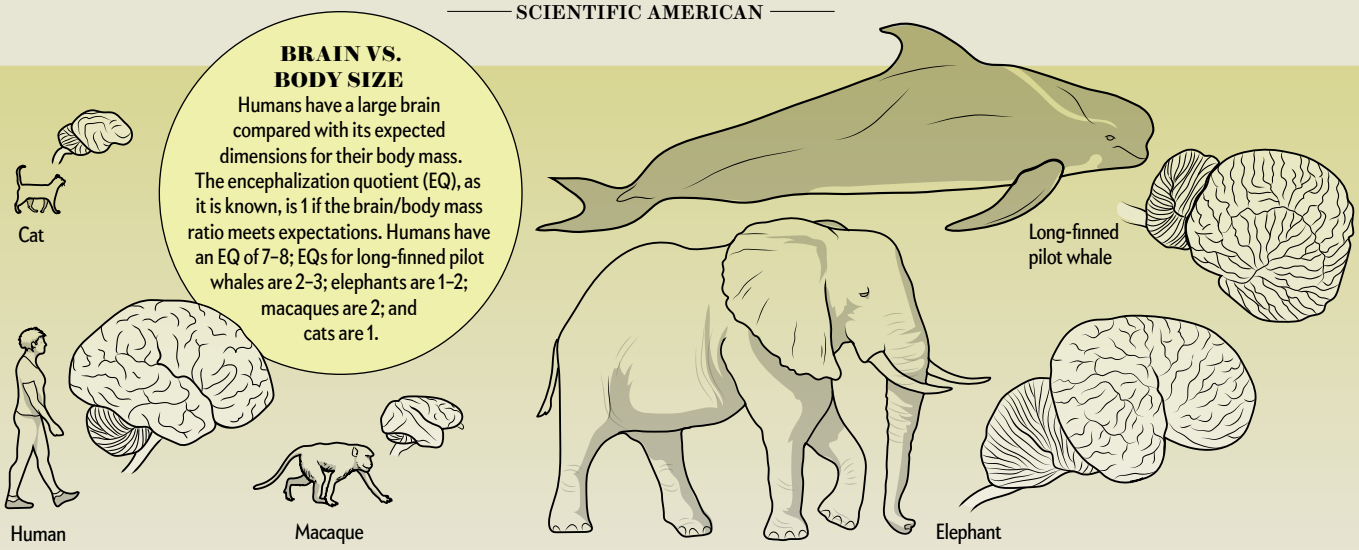
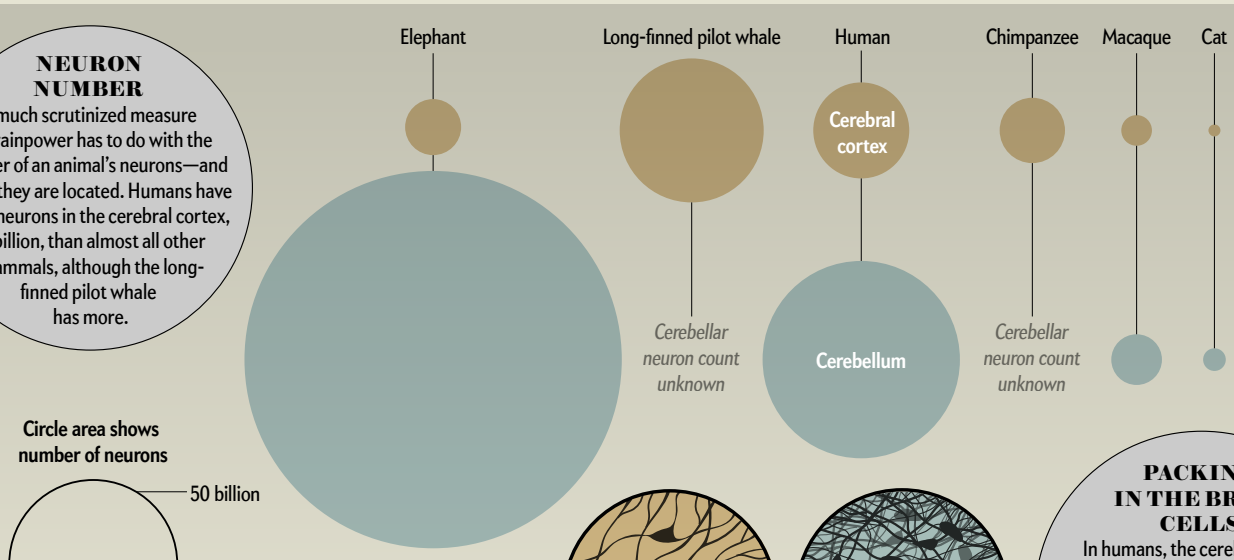
BRAIN VS. BODY SIZE

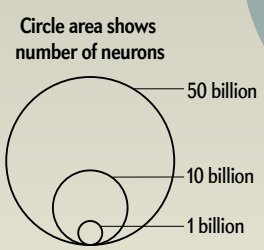
Humans have a large brain compared with its expected dimensions for their body mass. The encephalization quotient (EQ), as it is known, is 1 if the brain/body mass ratio meets expectations. Humans have an EQ of 7–8; EQs for long-finned pilot whales are 2–3; elephants are 1–2; macaques are 2; and cats are 1.

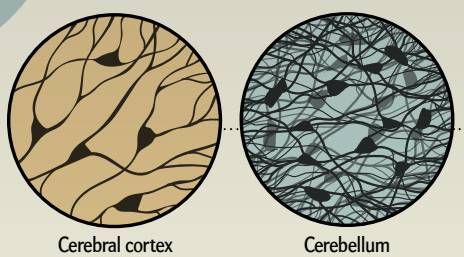


NEURON NUMBER

A much scrutinized measure of brainpower has to do with the number of an animal's neurons—and where they are located. Humans have more neurons in the cerebral cortex, 16 billion, than almost all other mammals, although the long-finned pilot whale has more.

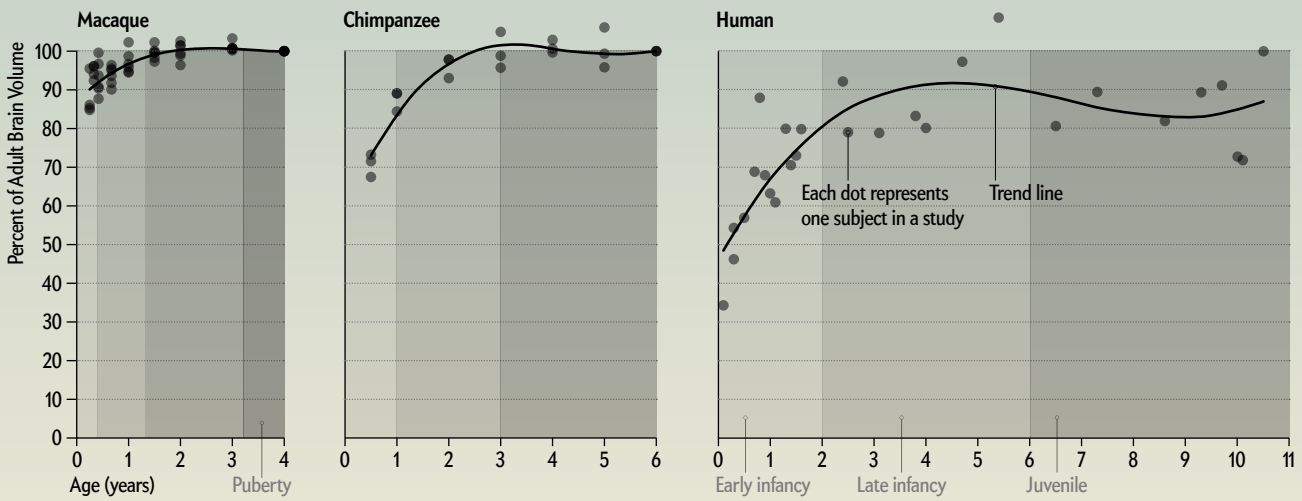






PACKING IN THE BRAIN CELLS

In humans, the cerebral cortex makes up 82 percent of the brain's mass but contains only 19 percent of the total neurons, whereas the cerebellum holds 80 percent or so of the neurons but only occupies 10 percent of its mass.



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How we learned to put our fate in one another's hands

By Michael Tomasello

Illustration by Yuko Shimizu

The Origins of Morality

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IF EVOLUTION IS ABOUT SURVIVAL OF THE FITTEST, HOW DID HUMANS EVER BECOME moral creatures? If evolution is all individuals maximizing their own fitness, how did humans come to feel that they really ought to help others and be fair to them?

There have traditionally been two answers to such questions. First, it makes sense for individuals to help their kin, with whom they share genes, a process known as inclusive fitness. Second, situations of reciprocity can arise in which I scratch your back and you scratch mine and we both benefit in the long run.

But morality is not just about being nice to kin in the manner that bees and ants cooperate in acts of inclusive fitness. And reciprocity is a risky proposition because at any point one individual can benefit and go home, leaving the other in the lurch. Moreover, neither of these traditional explanations gets at what is arguably the essence of human morality—the sense of obligation that human beings feel toward one another.

Recently a new approach to looking at the problem of morality has come to the fore. The key insight is a recognition that individuals who live in a social group in which everyone depends on everyone else for their survival and well-being operate with a specific kind of logic. In this logic of interdependence, as we may call it, if I depend on you, then it is in my interest to help ensure your well-being. More generally, if we all depend on one another, then we must all take care of one another.

How did this situation come about? The answer has to do with the particular circumstances that forced humans into ever more cooperative ways of life, especially when they are acquiring food and other basic resources.

IN BRIEF

Seeds of human morality were planted some 400,000 years ago, when individuals began to collaborate in hunting-and-gathering exploits. **Cooperative interaction** cultivated respect and fairness for other group members. **Growing population sizes** later cemented a sense of collective group identity that fostered a set of cultural practices and social norms.

THE ROLE OF COLLABORATION

OUR CLOSEST LIVING RELATIVES—chimpanzees and bonobos—forage for fruit and vegetation in small parties, but when resources are found, each individual scrambles to obtain food on its own. If any conflict arises, it is solved through dominance: the best fighter wins. In the closest thing to collaborative foraging among apes, a few male chimpanzees may surround a monkey and capture it. But this approach to hunting resembles more closely what lions and wolves do than the collaborative form of foraging undertaken by humans. Each chimpanzee maximizes its own chances in the situation by trying to block one possible avenue of the monkey's escape. The captor chimp will try to consume the entire carcass alone but typically cannot. Then all the individuals in the area converge on the captured prey and begin grabbing at it. The captor must allow this to happen or else fight the others, which would likely mean losing the food in the melee; thus, a small amount of food sharing takes place.

For a long time humans have done things differently. Around two million years ago the genus *Homo* emerged, with larger brains and new skills in making stone tools. Soon after, a global cooling and drying period led to a proliferation of terrestrial monkeys, which competed with *Homo* for many resources.

Early humans needed new options. One alternative involved scavenging carcasses killed by other animals. But then, according to an account from anthropologist Mary C. Stiner of the University of Arizona, some early humans—the best guess is *Homo heidelbergensis* some 400,000 years ago—began obtaining most of their food through active collaboration in which individuals formed joint goals to work together in hunting and gathering. Indeed, the collaboration became obligate (compulsory) in that it was essential to their survival. Individuals became interdependent with one another in immediate and urgent ways to obtain their daily sustenance.

An essential part of the process of obligate collaborative foraging involved partner choice. Individuals who were cognitively or otherwise incompetent at collaboration—those incapable of forming joint goals or communicating effectively with others—were not chosen as partners and so went without food. Likewise, individuals who were socially or morally uncooperative in their interactions with others—for example, those who tried to hog all the spoils—were also shunned as partners and so doomed. The upshot: strong and active social selection emerged for competent and motivated individuals who cooperated well with others.

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The key point for the evolution of morality is that early human individuals who were socially selected for collaborative foraging through their choice of partners developed new ways of relating to others. Most important, they had strong cooperative motives, both to work together to achieve common goals and to feel sympathy for and help existing or prospective partners. If an individual depended on partners for foraging success, then it made good evolutionary sense to help them whenever necessary to make sure they were in good shape for future outings. In addition, one's own survival depended on others seeing you as a competent and motivated collaborative partner. Thus, individuals became concerned with how others evaluated them. In experiments from our laboratory, even young children care about how they are being evaluated by others, whereas chimpanzees seemingly do not.

Absent a historical record and, in many cases, even evidence from fossil remains and archaeological artifacts, our lab in Leipzig, Germany, and others have investigated the origins of human thinking and morality by comparing the behaviors of our close primate relatives with those of young children who have yet to integrate the norms of their culture.

From these studies we have surmised that early humans who engaged in collaborative foraging developed a new kind of cooperative reasoning that led them to treat others as equally deserving partners—that is, not just with sympathy but also with a sense of fairness (based on an understanding of the equivalence between oneself and others). Partners understood that they could, in principle, take on any role in a collaboration and that both of them needed to work together for combined success. Moreover, as two individuals collaborated repeatedly with one another as foragers, they developed an understanding—a mental "common ground"—that defined the ideal way that each partner needed to fulfill a role for mutual success. These role-specific standards shaped the expectation of what each partner should do: For example, in hunting antelopes, the chaser must do X, and the spearer must do Y. These idealized standards were impartial in that they specified what either partner had to do to fulfill the role "properly" in a way that ensured joint success. The roles—each of which had mutually known and impartial standards of performance—were, in fact, interchangeable. As such, each partner on the hunt was equally deserving of the spoils, in contrast to cheats and free riders who did not lend a hand.

In choosing a partner for a collaborative effort, early humans wanted to pick an individual who would live up to an expected role and divide the spoils fairly. To reduce the risk inherent in partner choice, individuals who were about to become partners could use their newfound skills of cooperation to make a joint commitment, pledging to live up to their roles, which required a fair division of the spoils. As part of this commitment, the would-be partners also could pledge implicitly that whoever might renege on a commitment would be deserving of censure. (The box on the next page explains the evolution of morality within the framework of the philosophical concept of intentionality.)

Anyone who deviated from what was expected and wanted to stay in good cooperative standing would willingly engage in an act of self-condemnation—internalized psychologically as a sense of guilt. A "we is greater than me" morality emerged. During a collaboration, the joint "we" operated beyond the selfish individual level to regulate the actions of the collaborative partners "I" and "you."

The outcome of early humans' adaptations for obligate collaborative foraging, then, became what is known as a second-personal morality—defined as the tendency to relate to others with a sense of respect and fairness based on a genuine assessment of both self and others as equally deserving partners in a collaborative enterprise. This sense of fairness was heightened by the feeling of obligation, the social pressure to cooperate and to respect one's partner. That is, whereas all primates feel pressure to pursue their individual goals in ways they believe will be successful, the interdependency that governed social life for early humans meant that individuals felt pressures to treat others as they deserve to be treated and to expect others to treat them in this same way. This second-personal morality did not have all the defining attributes of modern human morality, but it already had the most important elements—mutual respect and fairness—in nascent form.

THE BIRTH OF CULTURAL NORMS

THE SECOND CRITICAL STEP in the evolution of human morality came when the small-scale collaborative foraging of early humans was eventually destabilized by two demographic factors that gave rise to modern humans more than 200,000 years ago. This new era came about because of competition among human groups. The struggles meant that loosely structured populations of collaborators had to turn into more tightly knit social groups to protect themselves from outside invaders. Each of these groups developed internal divisions of labor, all of which led to a collective group identity.

At the same time, population sizes were increasing. As numbers grew within these expanding tribal groups, the larger entities split into smaller subunits that still felt bound to the supergroup—or what might be characterized as a distinctive "culture." Finding ways to recognize members of one's own cultural group who were not necessarily next of kin—and then to separate them from members of other tribal groups—became essential. This type of recognition was important because only members of one's own cultural group could be counted on to share

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Evolution of Modern Human Morality

Animals often cooperate with others of their own species. But the way humans do so is different. The human form of cooperation—known simply as morality—distinguishes itself in two related ways. One person may help another based on unselfish motives driven by compassion, concern and benevolence. Also, members of a group might seek means for all to benefit through enacting norms to promote fairness, equity and justice. These capacities evolved over hundreds of thousands of years as humans began to work together out of a basic need for survival. The cognitive and social aspects of this process may be understood through the philosophical concept of intentionality: the ways individuals interpret the world and pursue their goals.

Individual Intentionality

An ability to flexibly change behavior to achieve a particular goal—usually for the purposes of competing with others—characterizes individual intentionality. Chimpanzee behavior is largely spurred by this self-interested perspective, as was that of the common ancestor of humans and chimpanzees—and perhaps it motivated early members of the hominin line as well. An example of this behavior occurs when chimpanzees forage for plants. A small group of animals searches together, but once they find fruit, each gathers its own stash and eats separately without interacting with other group members. A similar set of relatively self-centered behaviors are exhibited when hunting prey.

Joint Intentionality

Some 400,000 years ago a direct human ancestor—*Homo heidelbergensis*—began looking for better food sources. Hunting aurochs or other large game, as opposed to hares, required heightened cooperation, a joint intentionality, focusing on common goals. This type of teamwork contrasted with chimpanzees' every-animal-for-itself scramble during a monkey hunt. If the Paleolithic hunter-gatherers were to survive, their foraging practices became "obligate," not just a matter of discretion. Individuals chosen for the hunt were selected because they understood implicitly the need to cooperate and not hog the resulting spoils. A "second-personal morality" emerged in which it was understood that a "me" had to be subordinated to a "we."

Collective Intentionality

As groups grew in size beginning 150,000 years ago, the smaller bands that made up a tribe developed a set of common practices that represented the formal beginnings of human cultures. A set of norms, conventions and institutions grew up to define the group's goals and establish divisions of labor that set roles for each of its members—a collective intentionality that distinguished a tribe. These goals were internalized by each tribe member as an "objective morality" in which everyone knew immediately the difference between right and wrong as determined by the group's set of cultural practices.

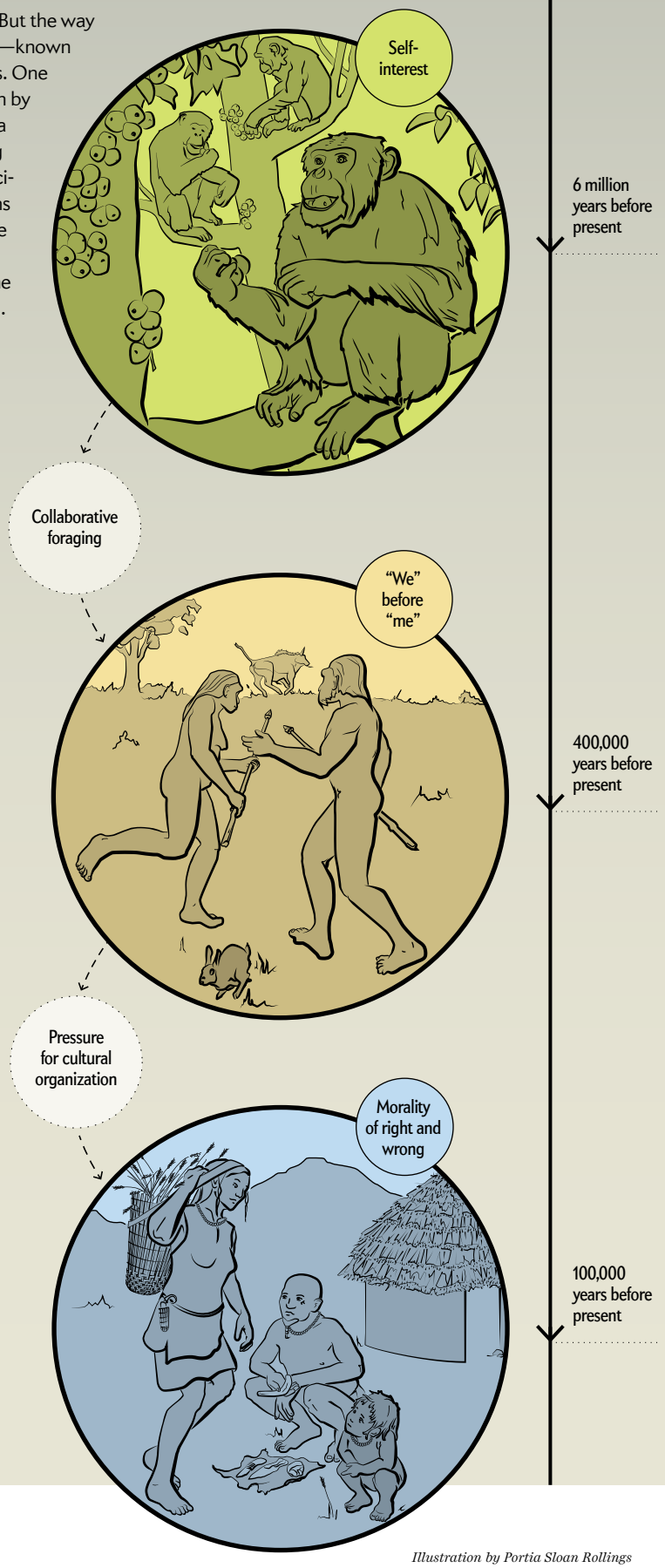

Illustration by Portia Sloan Rollings

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one's skills and values and be trustworthy partners, particularly for group defense. The dependence of individuals on the group thus led to a sense of collective identity and loyalty. A failure, meanwhile, to display this group identity and loyalty could result in being ostracized or dying in clashes with rivals.

Contemporary humans have many diverse ways of marking group identity, but the original ways were mainly behavioral ones and based on a number of assumptions: people who talk like me, prepare food like me and otherwise share my cultural practices are very likely members of my cultural group. And so from these suppositions emerged modern humans' tendency toward conformity to the group's cultural practices. Teaching one's children to do things in the conventional way defined by the group became mandatory for survival.

Teaching and conformity lay the foundations as well for cumulative cultural evolution—in which a practice or an artifact that had been in place for a long time could be improved on and that innovation could then be passed along to subsequent generations as part of a group's conventions, norms and institutions. Individuals were born into these collaborative social structures and had no choice but to conform to them. The key psychological characteristic of individuals adapted for cultural life was a group-mindedness, whereby people took the cognitive perspective of the group as a whole to care for its welfare and to conform to its ways—an inference derived from studies of the behavior of three-year-olds published in the late 2000s.

Individuals who belonged to a cultural group had to conform to the prevailing cultural practices and social norms to advertise that they identified with the group and its way of doing things. Some social norms were about more than conformity and group identity. They touched on a sense of sympathy and fairness (inherited from early humans), which became moral norms. Thus, just as some norms codified the right and wrong way of doing things in hunting or making tools, moral norms categorized the proper way of treating other people. Because the collective group goals and cultural common ground of human groups created an "objective" perspective—not "me" but "we" as a people—modern human morality came to be characterized as an objective form of right and wrong.

Of course, any individual could choose to act against a moral norm. But when called to task by other group members, the options were limited: one could ignore their criticism and censure and so place oneself outside the practices and values shared by the culture, perhaps leading to exclusion from the group. Modern humans thought of the cultural norms as legitimate means by which they could regulate themselves and their impulses and signal a sense of group identity. If a person did deviate from the group's social norms, it was important to justify uncooperativeness to others in terms of the shared values of the group ("I neglected my duties because I needed to save a child in trouble"). In this way, modern humans internalized not only moral actions but moral justifications and created a reason-based moral identity within the community.

THE PEOPLE OF WE

IN MY 2016 BOOK *A Natural History of Human Morality,* I proceed from the assumption that a major part of the explanation for human moral psychology comes from processes of evolution by means of natural selection. More important, though, the selecting is done not by the physical environment but rather by the social environment. In contrast to evolutionary approaches that base their arguments on reciprocity and the managing of one's reputation in the community, I emphasize that early human individuals understood that moral norms made them both judger and judged. The immediate concern for any individual was not just for what "they" think of me but rather for what "we," including "I," think of me. The essence of this account is thus a kind of "we is greater than me" psychological orientation, which gives moral notions their special powers of legitimacy in personal decision-making.

The challenge in the contemporary world stems from an understanding that humans' biological adaptations for cooperation and morality are geared mainly toward small group life or cultural groups that are internally homogeneous—with out-groups not being part of the moral community. Since the rise of agriculture some 10,000 years ago, human societies have consisted of individuals from diverse political, ethnic and religious lines.

As a consequence, it becomes less clear who constitutes a "we" and who is in the out-group. The resulting potential for divisiveness leads to both internal social tensions within a society and, at the level of nations, to outright war—the ultimate example of in- and out-group conflicts. But if we are to solve our largest challenges as a species, which threaten all human societies alike, we had best be prepared to think of all of humanity as a "we." SA

Michael Tomasello is a professor of psychology and neuroscience at Duke University and emeritus director of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany.

MORE TO EXPLORE

Cooperative Hunting and Meat Sharing 400–200 Kya at Qesem Cave, Israel. Mary C. Stiner et al. in *Proceedings of the National Academy of Sciences USA,* Vol. 106, No. 32, pages 13,207–13,212; August 11, 2009.

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The Naked Truth

Recent findings lay bare the origins of human hairlessness—and hint that naked skin was a key factor in the emergence of other human traits

By Nina G. Jablonski

AMONG PRIMATES, HUMANS ARE UNIQUE in having nearly naked skin. Every other member of our extended family has a dense covering of fur—from the short, black pelage of the howler monkey to the flowing copper coat of the orangutan—as do most other mammals. Yes, we humans have hair on our heads and elsewhere, but compared with our relatives, even the hairiest person is basically bare.

How did we come to be so denuded? Scholars have pondered this question for centuries. Finding answers has been difficult, however: most of the hallmark transitions in human evolution—such as the emergence of upright walking—are recorded directly in the fossils of our predecessors, but none of the known remains preserves impressions of human skin. In recent years, though, researchers have realized that the fossil record does contain indirect hints about our transformation from hirsute to hairless. Thanks to these clues and insights gleaned over the past decade or so from genomics and physiology, I and others have pieced together a compelling account of why and when humans shed their fur. In addition to explaining a very peculiar quirk of our appearance, the scenario suggests that naked skin itself played a crucial role in the evolution of other characteristic human traits, including our large brain and dependence on language.

HAIRY SITUATIONS

TO UNDERSTAND WHY our ancestors lost their body hair, we must first consider why other species have coats in the first place. Hair is a type of body covering that is unique to mammals. Indeed, it is a defining characteristic of the class: all mammals possess at least some hair, and most of them have it in abundance. It provides insulation and protection against abrasion, moisture, damaging rays of sunlight, and potentially harmful parasites and microbes. It also works as camouflage to confuse predators, and its distinctive patterns allow members of the same species to recognize one another. Furthermore, mammals can use their fur in social displays to indicate aggression or agitation: when a dog "raises its hackles" by involuntari-

IN BRIEF

Humans are the only primate species that has mostly naked skin. **Loss of fur** was an adaptation to changing environmental conditions that forced our ancestors to travel longer distances for food and water. **Analyses of fossils** and genes hint at when this transformation occurred. **The evolution** of hairlessness helped to set the stage for the emergence in our kind of large brains and symbolic thought.

GETTY IMAGES

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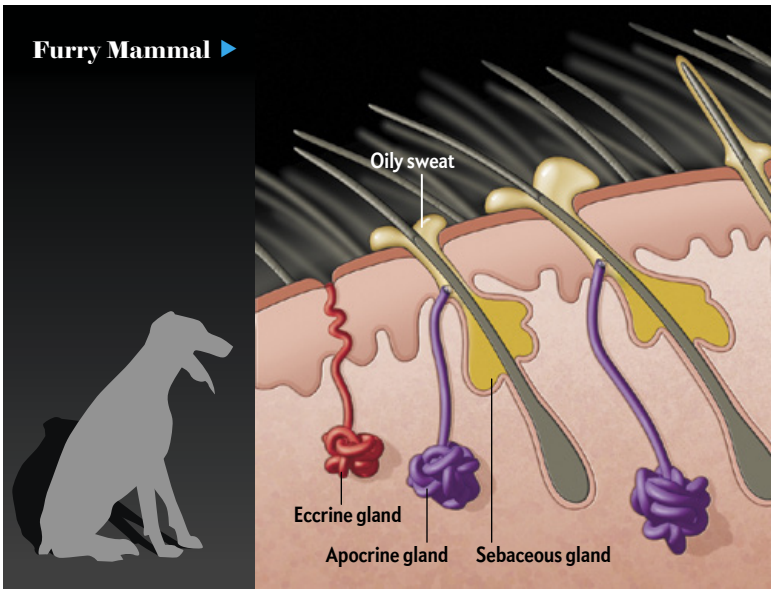
Furry vs. Naked

Naked human skin is better at ridding the body of excess heat than is fur-covered skin. Mammals possess three types of glands for the purpose: apocrine, eccrine and sebaceous. In most mammals the outermost layer of the skin, known as the epidermis, contains an abundance of apocrine glands. These glands cluster around hair follicles and coat the fur in a lather of oily sweat. Evaporation of this sweat, which cools the animal by drawing heat away from the skin, occurs at the surface of the fur. But the more the animal perspires, the less effectively it eliminates heat because the fur becomes matted, hampering evaporation. In the human epidermis, in contrast, eccrine glands predominate. These glands reside close to the skin surface and discharge thin, watery sweat through tiny pores. In addition to evaporating directly from the skin surface, this eccrine sweat vaporizes more readily than apocrine sweat, thus permitting improved cooling.



ly elevating the hairs on its neck and back, it is sending a clear signal to challengers to stay away.

Yet even though fur serves these many important purposes, a number of mammal lineages have evolved hair that is so sparse and fine as to serve no function. Many of these creatures live underground or dwell exclusively in the water. In subterranean mammals, such as the naked mole rat, hairlessness evolved as a response to living in large underground colonies, where the benefits of hair are superfluous because the animals cannot see one another in the dark and because their social structure is such that they simply huddle together for warmth. In marine mammals that never venture ashore, such as whales, naked skin facilitates long-distance swimming and diving by reducing drag on the skin's surface. To compensate for the lack of external insulation, these animals have blubber under the skin. In contrast, semiaquatic mammals—otters, for example—have dense, waterproof fur that traps air to provide positive buoyancy, thus decreasing the effort needed to float. This fur also protects their skin on land.

The largest terrestrial mammals—namely, elephants, rhinoceroses and hippopotamuses—also evolved naked skin because they are at constant risk of overheating. The larger an animal is, the less surface area it has relative to overall body mass and the harder it is for the creature to rid its body of excess heat. (On the flip side, mice and other small animals, which have a high surface-to-volume ratio, often struggle to retain sufficient heat.) During the Pleistocene epoch, which spans the time between two million and 10,000 years ago, the mammoths and other relatives of modern elephants and rhinoceroses were "woolly" because they lived in cold environments, and external insulation helped them conserve body heat and lower their food intake. But all of today's megaherbivores live in sweltering conditions, where a fur coat would be deadly for beasts of such immense proportions.

Human hairlessness is not an evolutionary adaptation to living underground or in the water—the popular embrace of the so-called aquatic ape hypothesis notwithstanding [*see box on opposite page*]. Neither is it the result of large body size. But our bare skin is related to staying cool, as our superior sweating abilities suggest.

SWEATING IT OUT

KEEPING COOL IS A BIG PROBLEM for many mammals, not just the giant ones, especially when they live in hot places and generate abundant heat from prolonged walking or running. These animals must carefully regulate their core body temperature because their tissues and organs, specifically the brain, can become damaged by overheating.

Mammals employ a variety of tactics to avoid burning up: dogs pant, many cat species are most active during the cooler evening hours, and many antelopes can off-load heat from the blood in their arteries to blood in small veins that has been cooled by breathing through the nose. But for primates, including humans, sweating is the primary strategy. Sweating cools the body through the production of liquid on the skin's surface that then evaporates, drawing heat energy away from the skin in the process. This whole-body cooling mechanism operates according to the same principle as an evaporative cooler (also known as a swamp cooler), and it is highly effective in preventing the dangerous overheating of the brain, as well as of other body parts.

Not all sweat is the same, however. Mammalian skin contains three types of glands—sebaceous, apocrine and eccrine—that together produce sweat. In most species, sebaceous and apocrine glands are the dominant sweat glands and are located near the base of hair follicles. Their secretions combine to coat hairs with an oily, sometimes foamy, mixture (think of the lather a racehorse generates when it runs). This type of sweat helps to cool the animal. But its ability to dissipate heat is limited. The late G. Edgar Folk, Jr., of the University of Iowa and his colleagues showed more than two decades ago that the effectiveness of cooling diminishes as an animal's coat becomes wet and

Illustration by Tami Tolpa (skin cross sections) and Jen Christiansen (dog and *human)*

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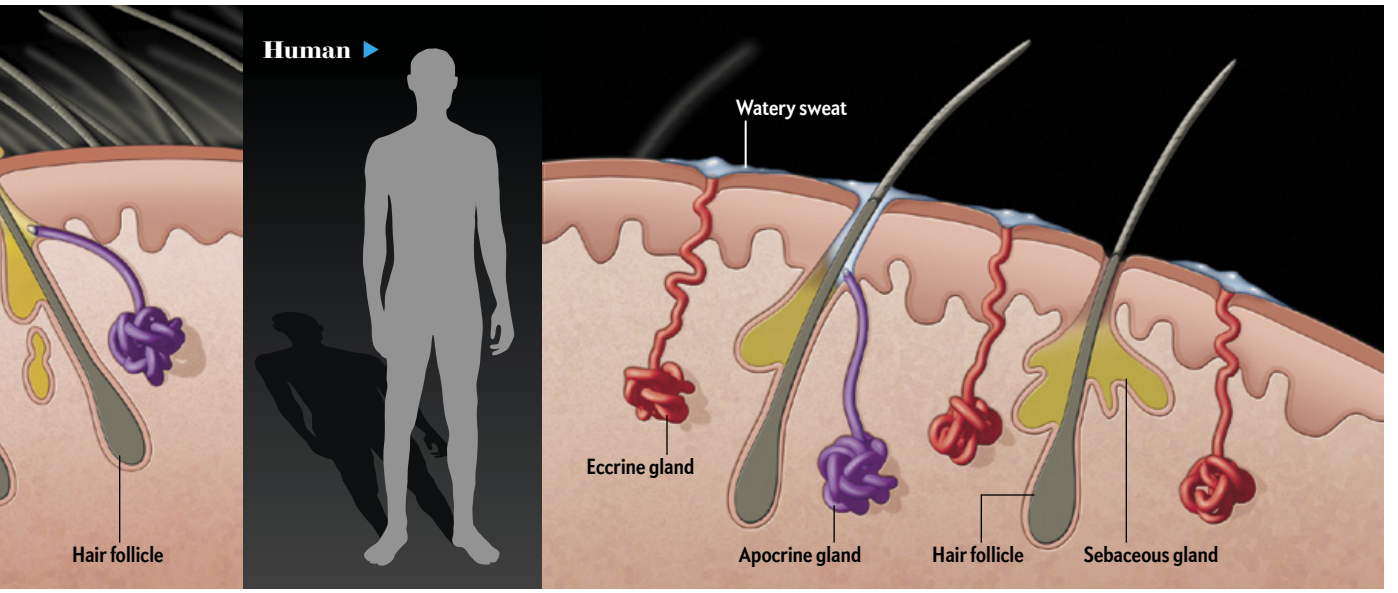

matted with this thick, oily sweat. The loss of efficiency arises because evaporation occurs at the surface of the fur, not at the surface of the skin itself, thus impeding the transfer of heat. Under conditions of duress, heat transfer is inefficient, requiring that the animal drink large amounts of water, which may not be readily available. Fur-covered mammals forced to exercise energetically or for prolonged periods in the heat of day will collapse from heat exhaustion.

Humans, in addition to lacking fur, possess an extraordinary number of eccrine glands—between two million and five million—that can produce up to 12 liters of thin, watery sweat a day. Eccrine glands do not cluster near hair follicles; instead they reside relatively close to the surface of the skin and discharge sweat through tiny pores. This combination of naked skin and watery sweat that sits directly atop it rather than collecting in the fur allows humans to eliminate excess heat very efficiently. Research by Daniel E. Lieberman of Harvard University and Dennis M. Bramble of the University of Utah showed that in humans the cooling system is so superior that in a marathon, on a hot day, a human could outcompete a horse.

Why the Aquatic Ape Theory Doesn't Hold Water

Among the many theories that attempt to explain the evolution of naked skin in humans, the aquatic ape theory (AAT)—which posits that humans went through an aquatic phase in their evolution—has attracted the most popular attention and support. First enunciated by English zoologist Sir Alister Hardy in a popular scientific article in 1960, the AAT later found a champion in writer Elaine Morgan, who promoted the theory in her lectures and writings before her death in 2013. The problem is, the theory is demonstrably wrong.

The AAT holds that around five million to seven million years ago tectonic upheavals in the Rift Valley of East Africa cut early human ancestors off from their preferred tropical forest environments. As a result, they had to adapt to a semiaquatic life in marshes, along coasts and in floodplains, where they lived for about a million years. Evidence of this aquatic phase, Morgan argued, comes from several anatomical features humans share with aquatic and semiaquatic mammals but not with savanna mammals. These traits include our bare skin, a reduced number of apocrine glands, and fat deposits directly under the skin.

The AAT is untenable for three major reasons. First, aquatic mammals themselves differ considerably in the degree to which they exhibit Morgan's aquatic traits. Thus, there is no simple connection between, say, the amount of hair an animal has and the environment in which it lives. Second, the fossil record shows that watery habitats were thick with hungry crocodiles and aggressive hippopotamuses. Our small, defenseless ancestors would not have stood a chance in an encounter with such creatures. Third, the AAT is overly complex. It holds that our forebears shifted from a terrestrial way of life to a semiaquatic one and then returned to living on terra firma full-time. As John H. Langdon of the University of Indianapolis has argued, a more straightforward interpretation of the fossil record is that humans always lived on land, where the driving force behind the evolution of naked skin was climate change that favored savanna grasslands over woodlands. And from a scientific perspective, the simplest explanation is usually the correct one. —*N.G.J.*

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Ancestors on the Move

Although the fossil record does not preserve any direct evidence of ancient human skin, scientists can estimate when nakedness evolved based on other fossil clues. Protohumans such as the australopithecines (*1*) probably led relatively sedentary lives, as today's apes do, because they lived in or near wooded environments rich in plant foods and freshwater. But as woodlands shrank and grasslands expanded, later ancestors, such as *Homo ergaster* (*2*), had to travel ever farther in search of sustenance—including meat. This species, which arose by 1.6 million years ago, was probably the first to possess naked skin and eccrine sweat, which would have offset the body heat generated by such elevated activity levels.

1 ***Australopithecus afarensis,*** **represented here by the 3.2-million-year-old Lucy fossil, was apelike in having short legs that were not well suited to traveling long distances.**

SHOWING SOME SKIN

BECAUSE HUMANS are the only primates that lack coats and have an abundance of eccrine glands, something must have happened since our hominin lineage diverged from the line leading to our closest living relative, the chimpanzee, that favored the emergence of naked, sweaty skin. Perhaps not surprisingly, the transformation seems to have begun with climate change.

By using fossils of animals and plants to reconstruct ancient ecological conditions, scientists have determined that starting around three million years ago the earth entered into a phase of global cooling that had a drying effect in East and Central Africa, where human ancestors lived. With this decline in regular rainfall, the wooded environments favored by early hominins gave way to open savanna grasslands, and the foods that our ancestors the australopithecines subsisted on—fruits, leaves, tubers and seeds—became scarcer, more patchily distributed and subject to seasonal availability, as did permanent sources of freshwater. In response to dwindling resources, our forebears would have had to abandon their relatively leisurely foraging habits for a much more consistently active way of life just to stay hydrated and obtain enough calories, traveling ever longer distances in search of water and edible plant foods.

It is around this time that hominins also began incorporating meat into their diet, as revealed by the appearance of stone tools and butchered animal bones in the archaeological record around 2.6 million years ago. Animal foods are considerably richer in calories than are plant foods, but they are rarer on the landscape. Carnivorous animals therefore need to range farther and wider than their herbivorous counterparts to procure a sufficient amount of food. Prey animals are also moving targets, save for the occasional carcass, which means predators must expend that much more energy to obtain their meal. In the case of human hunters and scavengers, natural selection morphed the apelike proportions of the australopithecines, who still spent some time in the trees, into a long-legged body built for sustained striding and running. (This modern form also no doubt helped our ancestors avoid becoming dinner themselves when out in the open.)

But these elevated activity levels came at a price: a greatly increased risk of overheating. Beginning in the 1980s, Peter Wheeler of Liverpool John Moores University in England published a series of papers in which he simulated how hot ancestral humans would have become out on the savanna. Wheeler's work, together with research my colleagues and I published in 1994, shows that the increase in walking and running, during which muscle activity builds up heat internally, would have required that hominins both enhance their eccrine sweating ability and lose their body hair to avoid overheating.

When did this metamorphosis occur? Although the human fossil record does not preserve skin, researchers do have a rough idea of when our forebears began engaging in modern patterns of movement. Studies conducted independently by Lieberman and Christopher Ruff of Johns Hopkins University have shown that by about 1.6 million years ago an early member of our genus called *Homo ergaster* had evolved essentially modern body proportions, which would have permitted prolonged walking and running. Moreover, details of the joint surfaces of the ankle, knee and hip make clear that these hominins actually exerted themselves in this way. Thus, according to the fossil evidence, the transition to naked skin and an eccrine-based sweating system must have been well underway by 1.6 million years ago to offset the greater heat loads that accompanied our predecessors' newly strenuous way of life.

Another clue to when hominins evolved naked skin has come

DENIS FINNIN AND JACKIE BECKETT *American Museum of Natural History (1 and 2)*

Illustrations by Victor Deak

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2 ***Homo ergaster*** **was the first hominin to possess long, striding legs, seen here in the 1.6-million-year-old Turkana Boy skeleton. Such elongated limbs facilitated sustained walking and running.**

from investigations into the genetics of skin color. In an ingenious study, Alan R. Rogers of the University of Utah and his colleagues examined sequences of the human *MC1R* gene, which is among the genes responsible for producing skin pigmentation. The team showed that a specific gene variant always found in Africans with dark pigmentation originated as many as 1.2 million years ago. Early human ancestors are believed to have had pinkish skin covered with black fur, much as chimpanzees do, so the evolution of permanently dark skin was presumably a requisite evolutionary follow-up to the loss of our sun-shielding body hair. Rogers's estimate thus provides a minimum age for the dawn of nakedness.

SKIN DEEP

LESS CERTAIN THAN WHY and when we became naked is how hominins evolved bare flesh. The genetic evidence for the evolution of nakedness has been difficult to locate because many genes contribute to the appearance and function of our skin. Nevertheless, hints have emerged from large-scale comparisons of the sequences of DNA "code letters," or nucleotides, in the entire genomes of different organisms. Comparison of the human and chimp genomes reveals that one of the most significant differences between chimp DNA and our own lies in the genes that code for proteins that control properties of the skin. The human versions of some of those genes encode proteins that help to make our skin particularly waterproof and scuff resistant—critical properties, given the absence of protective fur. This finding implies that the advent of those gene variants contributed to the origin of nakedness by mitigating its consequences.

The outstanding barrier capabilities of our skin arise from the structure and makeup of its outermost layer, the stratum corneum (SC) of the epidermis. The SC has what has been described as a bricks-and-mortar composition. In this arrangement, multiple layers of flattened dead cells, called corneocytes, which contain the protein keratin and other substances, are the bricks; ultrathin layers of lipids surrounding each of the corneocytes make up the mortar.

Most of the genes that direct the development of the SC are ancient, and their sequences are highly conserved among vertebrates. That the genes undergirding the human SC are so distinctive signifies, therefore, that the advent of those genes was important to survival. New research by Pramod Gautam, Vivek Natarajan and colleagues at the Academy of Scientific and Inno-

Beating the Heat

Naked skin is not the only adaptation humans evolved to maintain a healthy body temperature in the sweltering tropics where our ancestors lived. They also developed longer limbs, increasing their surface-to-volume ratio, which in turn facilitated the loss of excess heat. That trend seems to be continuing even today. The best evidence of this sustained adaptation comes from populations in East Africa, such as the Dinka of southern Sudan. It is surely no coincidence that these people, who live in one of the hottest places on earth, also have extremely long limbs.

Why do modern humans exhibit such a wide range of limb proportions? As our forebears migrated out of tropical Africa into cooler parts of the world, the selection pressures changed, allowing for a variety of body shapes to evolve.

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SOCIAL SIGNALING is an important function of fur—from raised hackles indicating aggression to coat patterns that help members of the same species to recognize one another (*1*). We humans compensate for our lack of fur by decorating our bodies with tattoos (*2*), jewelry and other adornments. We also have complex facial expressions (*3*), as well as the ability to convey our emotions through language (*4*).

vative Research in Delhi, India, is revealing that genes encoding keratin production and those responsible for differentiation of the epidermis are under accelerated evolution in the human lineage and that this trend appears to be driven by the diverse environmental circumstances in which people live. The exciting connection between the evolution of the protein building blocks of the human skin and the physical environment speaks to the fact that our skin has been the primary interface between our bodies and the physical environment for much of our evolution.

Another question we are eager to answer is how human skin came to contain such an abundance of eccrine glands. We have known for a long time that this had something to do with the genes that determine the fate of epidermal stem cells, which are unspecialized, in the embryo. Early in development, groups of epidermal stem cells in specific locations interact with cells of the underlying dermis, and genetically driven chemical signals within these niches direct the differentiation of the stem cells into hair follicles, eccrine glands, apocrine glands, sebaceous glands or plain epidermis. Recent research by Catherine Pei-Ju Lu, Elaine Fuchs and their colleagues at the Rockefeller University has shed important light on this topic. Using genome-wide analyses and functional studies, they showed that sweat glands and hair follicles are specified by different factors that signal the activity of groups of cells within the stem cell niches of the skin. A different pattern of signals determines whether sweat glands or hairs will be produced. These signals can be thought of as a developmental "switch" because they determine the fate of the epidermal stem cells at a specific time in embryonic development. Knowing how eccrine sweat glands are specified during development is a critical first step in understanding when eccrine glands came to dominate the surface of human skin and play such an important role in thermoregulation.

Of Lice and Men

Researchers have looked to lice for clues to why humans lost their body hair. In 2003 Mark Pagel of the University of Reading in England and Walter Bodmer, now head of the Cancer and Immunogenetics Laboratory at the University of Oxford, proposed that humans shed their fur to rid their bodies of disease-spreading lice and other fur-dwelling parasites and to advertise the health of their skin. Other investigators have studied head and body lice for insight into how long after becoming bare-skinned our ancestors began to cover up with clothing.

Although body lice feed on blood, they live on clothing. Thus, the origin of body lice provides a minimum estimate for the dawn of hominin garb. By comparing gene sequences of organisms, investigators can learn roughly when the species arose. Such analyses in lice indicate that whereas head lice have plagued humans from the start, body lice evolved much later. The timing of their appearance hints that humans went naked for more than a million years before getting dressed.

NOT ENTIRELY NUDE

HOWEVER IT WAS THAT we became naked apes, evolution did leave a few body parts covered. Any explanation of why humans lost their fur therefore must also account for why we retain it in some places. Hair in the armpits and groin probably serves both to propagate pheromones (chemicals that serve to elicit a behavioral response from other individuals) and to help keep these areas lubricated during locomotion. As for hair on the head, it was most likely retained to help shield against excess heat on the top of the head. That notion may sound paradoxical, but having dense hair on the head creates a barrier layer of air between the sweating scalp and the hot surface of the hair. Thus, on a hot, sunny day the hair absorbs the heat while the barrier layer of air remains cooler, allowing sweat on the scalp to evaporate into that layer of air. Tightly curled hair provides the optimum head covering in this regard because it increases the thickness of the space between the surface of the hair and the scalp, allowing air

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to blow through. Much remains to be discovered about the evolution of human head hair, but it is possible that tightly curled hair was the original condition in modern humans and that other hair types evolved as humans dispersed out of tropical Africa.

With regard to our body hair, the question is why it is so variable. There are many populations whose members have hardly any body hair at all and some populations of hirsute folks. Those with the least body hair tend to live in the tropics, whereas those with the most tend to live outside the tropics. Yet the hair on these nontropical people provides no warmth to speak of. These differences in hairiness clearly stem to some extent from testosterone because males in all populations have more body hair than females do. A number of theories aimed at explaining this imbalance attribute it to sexual selection. For example, one posits that females prefer males with fuller beards and thicker body hair because these traits occur in tandem with virility and strength. Another proposes that males have evolved a preference for females with more juvenile features. These are interesting hypotheses, but no one has actually tested them in a modern human population. In the absence of any empirical evidence, it is still anybody's guess why human body hair varies the way it does.

NAKED AMBITIONS

GOING FURLESS WAS NOT merely a means to an end; it had profound consequences for subsequent phases of human evolution. The loss of most of our body hair and the gain of the ability to dissipate excess body heat through eccrine sweating helped to make possible the dramatic enlargement of our most temperature-sensitive organ, the brain. Whereas the australopithecines had a brain that was, on average, 400 cubic centimeters—roughly the size of a chimp's brain—*H. ergaster* had a brain twice that large. And within a million years the human brain swelled another 400 cubic centimeters, reaching its modern size. No doubt other factors influenced the expansion of our gray matter—the adoption of a sufficiently caloric diet to fuel this energetically demanding tissue, for example. But shedding our body hair was surely a critical step in becoming brainy.

Our hairlessness also had social repercussions. Although we can technically raise and lower our hackles when the small muscles at the base of our hair follicles contract and relax, our body hairs are so thin and wispy that we do not put on much of a show compared with the displays of our cats and dogs or of our chimpanzee cousins. Neither do we have the built-in advertising—or camouflage—offered by zebra stripes, leopard spots, and the like. Indeed, one might even speculate that universal human traits such as social blushing and complex facial expressions evolved to compensate for our lost ability to communicate through our fur. Likewise, body paint, cosmetics, tattoos and other types of skin decoration are found in various combinations in all cultures because they convey group membership, status and other vital social information formerly encoded by fur. We also employ body postures and gestures to broadcast our emotional states and intentions. And we use language to speak our mind in detail. Viewed this way, naked skin did not just cool us down—it helped make us who we are. SA

Nina G. Jablonski is Evan Pugh University Professor of Anthropology at Pennsylvania State University. Her research focuses on the natural history of human skin, the origin of bipedalism, the evolution and biogeography of Old World monkeys, and the paleoecology of mammals that lived during the past two million years. She has conducted fieldwork in China, Kenya and Nepal.

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SCALARIFORM, or ladder-shaped, symbol on the wall of La Pasiega cave in northern Spain has been dated to nearly 65,000 years ago, which means it must have been painted by a Neandertal. Shown in detail on page 90.

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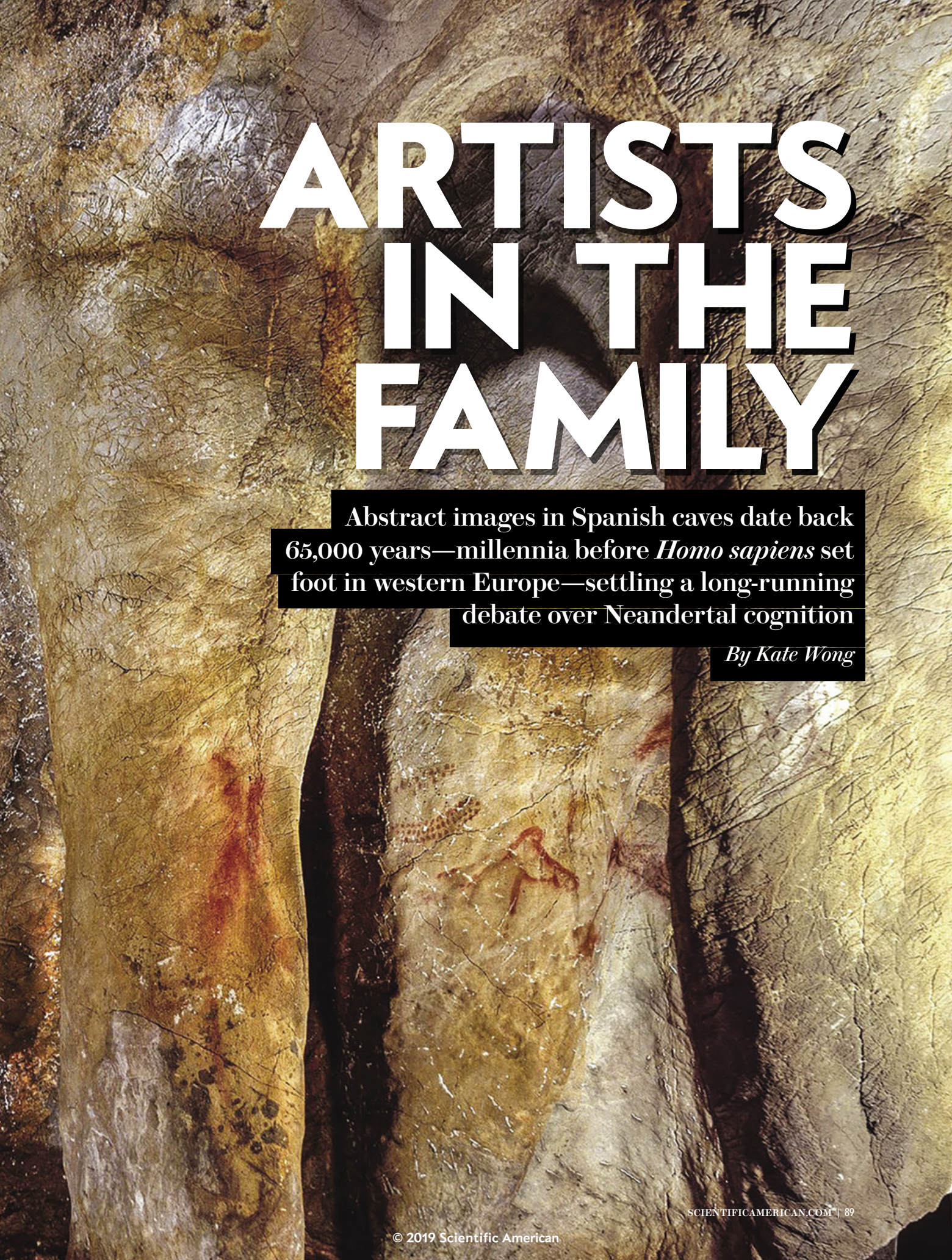

ARTISTS IN THE FAMILY

Abstract images in Spanish caves date back 65,000 years—millennia before *Homo sapiens* set foot in western Europe—settling a long-running debate over Neandertal cognition

By Kate Wong

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ONCE UPON A TIME, IN the dim recesses of a cave in what is now northern Spain, an artist carefully applied red paint to the cave wall to create a geometric design—a ladder-shaped symbol composed of vertical and horizontal lines. In another cave hundreds of kilometers to the southwest, another artist pressed a hand to the wall and blew red paint around the fingers to create a stenciled handprint, working by the flickering firelight of a torch or oil lamp in the otherwise pitch darkness. In a third cave, located in the far south, curtainlike calcite formations were decorated in shades of scarlet.

Although nothing of the artists themselves remains to establish their identity, archaeologists have long assumed cave painting was the sole purview of *Homo sapiens*. Another group of large-brained humans, the Neandertals, lived in the right time and place to be the creators of some of the cave art in Europe. But only *H. sapiens* had the cognitive sophistication needed to develop symbolic behavior, including art. Or so many experts thought.

Now dates obtained for the images in these three Spanish caves could put that enduring notion to rest. In a paper published in 2018 in *Science,* researchers reported some of the images are far older than the earliest known fossils of *H. sapiens* in western Europe, suggesting that they were instead created by Neandertals. The findings open a new window into the minds of these oft-maligned cousins of ours. They also raise key questions about the origin of symbolic thought and what, exactly, distinguishes *H. sapiens* from other members of the human family.

The dating results come as a vindication long in the making for Neandertals, who have had an image problem ever since the early 1900s, when French paleontologist Marcellin Boule famously reconstructed a Neandertal skeleton from the site of La Chapelle-aux-Saints in France as an apelike brute. In the decades that followed scientists discovered that Neandertals were much more like us physically than Boule had surmised. They also found Neandertals and *H. sapiens* made the same kinds of stone tools for millennia—but the bad rap stuck.

For a long time arguably the most significant point of distinction between Neandertals and modern humans seemed to be that Neandertals did not make or use symbols. Whereas *H. sapiens* left behind jewelry, sculptures and cave paintings—all products of symbolic thought—no such items could be unequivocally attributed to Neandertals. In recent years, however, evidence for Neandertal symbolic behavior has been accumulating from sites throughout Europe. In Gibraltar a Neandertal engraved a hashtaglike symbol in the bedrock of a cave. In Croatia Neandertals harvested eagle talons and appear to have fashioned them into necklaces. At sites in Gibraltar and Italy they hunted birds for their feathers, perhaps to wear as ceremonial headdresses and capes. In Spain, they made shell jewelry and mixed sparkly paint that they may have used as a kind of cosmetic. In a cave in France Neandertals erected semicircular walls of stalagmites, possibly for some ritual purpose. The list goes on.

Still, a key form of symbolic expression appeared to be missing from the Neandertal repertoire: rock art. The spectacular cave paintings of woolly rhinos, mammoths and other ice age animals at famous sites such as Chauvet and Lascaux in France, among other examples, were all linked to early modern humans. In the absence of any unambiguous evidence to the contrary, scientists assumed all cave paintings everywhere were likewise the handiwork of *H. sapiens*.

But in 2012 researchers led by archaeologist Alistair Pike, now

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at the University of Southampton in England, made a discovery that challenged this assumption. The team dated dozens of paintings from caves in Spain and found several that were rather older than previously thought. One image, a red disk in El Castillo cave, was found to have a minimum age of 40,800 years—old enough to possibly be the work of a Neandertal and almost too old to be a modern human creation. (*H. sapiens* is not thought to have reached western Europe until around 42,000 years ago.) At a press conference announcing the 2012 findings, study co-author João Zilhão of the University of Barcelona declared any art from Europe that is found to be more than 42,000 years old must be attributed to Neandertals.

Six years later that day came. In the 2018 study Pike, Zilhão and their colleagues dated paintings in three caves located in different regions of Spain: La Pasiega in Cantabria, Maltravieso in Extremadura and Ardales in Andalucía. Although the caves contain a mix of figurative and nonfigurative images, the researchers focused their efforts on the latter variety. "We found in our 2012 study that the earliest dates we were getting were on red nonfigurative art—lines, dots, symbols and hand-stencils—so for [this] project we focused on paintings similar to these," Pike explains.

FOR A LONG TIME ARGUABLY THE MOST SIGNIFICANT POINT OF DISTINCTION BETWEEN NEANDERTALS AND MODERN HUMANS SEEMED TO BE NEANDERTALS DID NOT MAKE OR USE SYMBOLS.

As in the 2012 study, the team determined the age of the paintings using a radiometric technique called uranium-thorium dating, which is based on the radioactive decay of uranium into thorium over time. Specifically, the researchers obtained samples of the thin crusts of carbonate that have formed on top of the paintings and analyzed their thorium content to gauge the age of the crust, which provides a minimum age for the underlying painting. Their efforts were richly rewarded: The analyses show all three caves contain paintings dating to at least 64,800 years ago. Neandertals across Spain were thus making rock art more than 20,000 years before modern humans set foot in western Europe.

Outside researchers praised the new study. "Wow!" says Genevieve von Petzinger, a Ph.D. candidate at the University of Victoria in British Columbia whose research focuses on prehistoric symbols. She notes that when Pike and his collaborators raised the possibility of Neandertal artists in 2012, they got a lot of static from their peers who argued there was no reason to credit Neandertals over modern humans for the El Castillo images. "This is the mic drop," Petzinger says of the newly dated paintings. "At 65,000, there's no way it's modern humans."

Not only do the dates point to Neandertals making the art, they indicate Neandertals came up with these ideas on their own. When archaeologists first began uncovering signs of Neandertal symbolism, the evidence all came from the tail end of the Neandertals' reign, by which point modern humans had established themselves in Europe. Some researchers posited that Neandertals were simply copying their modern human neighbors, possibly without really understanding what they were doing.

The new dates have convinced proponents of this idea otherwise. "I think the most parsimonious explanation on current evidence is that it is Neandertals that must be making these representations," speculates Thomas Higham of the University of Oxford, who has been dating sites across Europe to develop a chronology of the displacement of Neandertals by modern humans and who was not involved in the new study. "I say that as someone who has long held the view that incoming modern humans, overlapping with Neandertals upon arrival [around] 45,000 to 40,000 years ago, were responsible for the late development of Neandertal symbolic behavior—perhaps a kind of 'imitation without understanding'—just before their disappearance."

Could the ancient paintings instead signal *H. sapiens* reached this part of Europe earlier than the fossil record indicates? After all, recent discoveries elsewhere in the world have suggested our species originated and began spreading out of Africa thousands of years earlier than previously thought. "It's possible," Higham says, "but there is no evidence for it yet." If Neandertals had cave painting traditions, then researchers will need to grapple with the question of whether their behavior actually differed from that of modern humans in any meaningful way. One school of thought holds moderns were able to displace Neandertals by virtue of superior intellect and symbolic capabilities, including language.

Some experts have dismissed previous examples of Neandertal art, such as the Gibraltar hashtag engraving, as predictably unimpressive compared with the figurative art modern humans made. Von Petzinger disagrees. "When researchers joke about the sophistication of Neandertal art, I think they're missing the point," she says. "The big cognitive leap is making the graphic mark; it's the ability to store information outside the body." In a general sense, she says, the creation of abstract signs "marks the first step toward written language."

"What is now needed is a wide-ranging analysis of other cave art using the same techniques to explore other potential cases," Higham says. Pike and his team are looking to do exactly that. "Hand stencils of dots and disks are found in caves all over Europe," Pike notes. "We would like to start dating art outside Spain to see if Neandertal painting was as widely distributed as Neandertals were." SA

Kate Wong is a senior editor for evolution and ecology at *Scientific American*.

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THE EVO

Do humans dance just for fun, or did it help our ancestors survive thousands of years ago?

By Thea Singer

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LUTION OF DANCE

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THE ARGENTINE TANGO IS FAMOUS for being a difficult but electrifying dance. Just one look at a performance by professional dancers Mora Godoy and José Lugones shows why. Whether dancing chest to chest or obliquely angled, Godoy and Lugones whip across the floor, legs whirring like blades on a fan. When she raises a bent leg forward, he answers with a quick kick aft. The pair slip easily between the two- and four-beat phrasing of the music, perfectly matching each other's every hip swivel and toe tap, leg lick and foot volley.

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Not everyone can move with the fiery grace of this expert duo, of course. But we have all felt the call to dance, which has beckoned countless participants across all cultures throughout human history. Yet dance is rare in the animal kingdom. And although a few other species can move their bodies to a beat, none of them exhibits anything like the complexity seen in human dancing.

Why should dancing be such a common human trait, and why are we so good at it? In recent years scientists have begun to identify features of the brain and body that underpin our exceptional ability. Some of these features are linked to language and upright locomotion, two traits that have contributed significantly to the success of the human lineage. Perhaps, then, dance is a happy evolutionary accident, a by-product of natural selection for those other traits that helped our ancestors thrive. Insights from psychology and archaeology hint at another intriguing possibility, however: that dancing itself evolved as an adaptive trait, one that may have strengthened human social bonds in ways that enhanced survival.

SENSE THE BEAT

BROKEN DOWN to its basic elements, dancing is the act of sensing and predicting the timing of an external beat and then matching that beat with rhythmic movements of the body. These actions require a great deal of coordination among different parts of the brain.

Over the past decade researchers in Canada, the U.S. and England have begun to identify networks of nerve cells deep within the human brain that act in concert to isolate the beat from external auditory signals. Once these networks recognize the underlying pattern, they predict the timing of subsequent beats, essentially generating a matching arrangement within the brain.

The next step is what makes dancing possible. The parts of

IN BRIEF

Dance plays an important role in every human society known to researchers. Does its ubiquity imply a survival advantage, or is it merely an accidental by-product of large brains and upright posture?
The ability to dance depends on a neurological process in which so-called motor neurons that control the muscles align, or entrain, with the auditory signals detected by sensory neurons.
Until recently, investigators assumed that only humans possessed the ability to entrain. But parrots and a California sea lion have also demonstrated this talent.
Further investigations in a range of disciplines reveal that the origins of dance are complex and may never be fully understood.

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the brain that control the muscles start to fire in conjunction with the predicted beats from the auditory networks. (Indeed, these so-called motor-planning areas of the brain kick into action even when we stand still and merely *perceive* a beat.) This coupling of auditory processing with rhythmic physical movement lies at the heart of our ability to tap out a beat with our fingers or to waltz across the floor. Scientists call it "entrainment."

Barring illness, we humans come by entrainment naturally, and we can sustain a diverse repertoire of rhythmic movement across a wide range of tempos for long periods. "Our synchronization abilities are incredibly flexible," asserts Aniruddh D. Patel, a neuroscientist at Tufts University. "We can stay synchronized to a beat whether it slows down or speeds up by plus or minus 30 percent." This capacity generally emerges between three and five years of age.

For years scientists believed that only humans had the ability to entrain their physical behavior with external sounds. Then, in 2009, studies started to emerge showing that parrots and perhaps songbirds can—to a limited extent—time their movements to music as well. Snowball, a male cockatoo famous for bobbing his head up and down in time to music from the Backstreet Boys, was among the birds studied. Indeed, in a new study published in July 2019, Patel and his colleagues report that Snowball went far beyond just bobbing his head in time to a musical beat. Over a period of 23 minutes, the researchers filmed Snowball performing 14 different dance movements using a variety of body parts to the pop songs "Another One Bites the Dust" and "Girls Just Wanna Have Fun." This indicates that, as with humans, Snowball's movement to music involves contributions from motor-planning regions of the brain as well as auditory ones. "Snowball developed this behavior without any training," Patel says. "That suggests that dancing to music isn't an arbitrary product of human culture but a response to music that arises when certain cognitive and neural capacities come together in animal brains." And in 2013 researchers reported that a California sea lion named Ronan could move her head to a range of tempos.

Humans are, however, the only animals that can produce the closely coordinated movements required of partner or group dancing. Birds that can entrain move in spurts to music on their own, Patel says. Even when multiple parrots live together in a shelter, he says, they do not coordinate their movements or dance with one another.

WORLD BEAT: Children perform a classical dance in Mumbai, India (*1*); break-dancers in Los Angeles demonstrate moves (*2*); modern ballet dancers show flexibility and grace (*3*); Bolshoi ballet lines up perfectly (*4*); street parade and festive dance in Cuba (*5*).

IMITATION GAME

DANCE IS NOT the only human attribute that depends on entrainment. Speech and singing also require the ability to match sound with physical movement—specifically, of the vocal cords and muscles in the throat. Tracing the neural pathways involved in vocalization gave Patel an idea about how entrainment between nerves that process sound and those that control muscles might have evolved. His work suggests that the same neural innovations that allowed humans to learn and produce spoken language also predisposed us to be dancers.

In Patel's view, the ability to mimic sounds paved the way for predictive, flexible entrainment. Such mimicry demonstrates what researchers call "vocal learning," in which an animal listens carefully to a sound, forms a mental model of it, aligns the motor control of its throat, tongue and mouth with that model, and then produces the modeled sound. When the animal listens to the output, it notes and corrects discrepancies between the predicted and the actual sound and tries again. Patel suggests that the coupling of auditory and motor processing required to imitate sounds laid the neurological groundwork for the later, more complex process of predictive auditory-motor entrainment.

Why might vocal learning have evolved in select animals? Some scientists speculate that it might have enabled songbirds to master complex acoustic displays to advertise for a mate. In parrots, Patel says, it furnished an "acoustic badge—something that marks them as a member of a group."

If Patel's hypothesis that vocal mimicry is a necessary precondition for auditory-motor entrainment is right, then the only animals that should be able to entrain are those that are already capable of imitating sounds. To date, the only animals that are known to imitate external sounds are humans, hummingbirds, parrots, songbirds, whales, certain flipper-footed marine mammals (pinnipeds), elephants and some bats. Meanwhile our nearest living relatives, bonobos and chimpanzees, are not vocal learners, and most evidence to date suggests that they do not entrain. Although one chimp in a study was apparently able to synchronize her taps with the beat at one tempo, she could not keep the beat at other tempos. Researchers also found one bonobo that seemed to be able to drum to a beat, but they caution that she might have been watching the tester for cues rather than just responding to what she was hearing.

GETTY IMAGES (3); LINDA VARTOOGIAN *Getty Images (4)*; ADALBERTO ROQUE *Getty Images (5)*

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Such observations support the idea that vocal mimicry might be a necessary precursor for entrainment. That Snowball exhibited a diverse repertory of movement underscores that idea. But the concept is by no means a slam dunk. Demonstrating entrainment in nonhuman species is not easy. Think of the complicated duets between some species of songbirds. Do they take turns singing by keeping time—predicting when the other will finish—or are they merely reacting to their partner's silence? And how could you possibly test this?

The biggest problem for Patel's vocal-mimicry hypothesis, however, is Ronan, the head-bobbing sea lion. Sea lions are not known to be vocal learners, although they are related to walruses and seals, which are. Yet in 2013 researchers at the University of California, Santa Cruz, demonstrated that Ronan could move her head in time with simple beats and, later, more complex music. Further tests showed that she could correctly keep time with the beat even when it sped up or slowed down.

There are several ways to explain Ronan's apparent ability. Maybe she is just one very gifted sea lion—the exception that proves the rule. Or perhaps sea lions still possess the neural machinery for vocal mimicry and just no longer use it.

It is possible, of course, that Ronan's feat proves the vocal-mimicry hypothesis wrong. Patel and others have suggested that one way to test this hypothesis would be to determine whether horses—which are neither vocal learners nor related to them—can also be taught to entrain. Horses "should not be able to match a specific tempo, but there is widespread anecdotal evidence that they can," says Mara Breen, an assistant professor of psychology at Mount Holyoke College, who is testing Patel's hypothesis in horses. If it turns out that these animals can entrain, then perhaps the process is not so hard after all, or it evolved in other species for different reasons than it did in humans.

GLOBAL REACH: Traditional dancers in Rwanda (*6*); teenagers strike a pose in the U.S. (*7*); Jewish dancers celebrate in London (*8*); Sufi dancers whirl in Istanbul (*9*); Geisha performers display fans in Japan (*10*); dancers do the rumba in Cuba (*11*).

A ROLE FOR RUNNING?

UNLIKE DANCE in other creatures, human dance goes beyond head bobbing to include coordinated movement of the torso and limbs. How might the evolution of our unusual upright posture have affected our capacity for dance? One idea that has gained attention in recent years is that dance could have grown out of our ability to run—as opposed to just walk—on two legs. "Certainly we take advantage of being bipedal to dance," says Harvard University evolutionary biologist Daniel E. Lieberman, who, in 2004, co-authored a seminal paper in *Nature* on the role of endurance running in human evolution. But that differs from what humans *evolved* to do. "We evolved to walk and to run, to throw, to dig," Lieberman says. Natural selection for these abilities enabled our ancestors—in particular, *Homo erectus*—to upgrade their hunting and foraging skills.

"There are all kinds of fascinating adaptations that we think evolved for running," Lieberman continues. The toes of modern humans are much shorter, for example, than those of our forebears. From a biomechanical point of view, this is unnecessary for walking, but it makes running more efficient. The three semicircular canals of the inner ear have grown larger over the course of millennia, allowing us to maintain our balance whenever we move our head, so that we can move with greater speed and agility. Such adaptations are also useful for dancing.

In Lieberman's view, dance could be a coincidental outgrowth of the evolution of running that proved so useful it conferred its own additional selective advantage. "It doesn't have to be an all-or-nothing thing," he says. "It can be partial. It could be that dancing was selected for, or it could be that dancing was never selected for, or it could be that certain elements of dancing were selected for." He pauses. "Testing those hypotheses—boy, that is hard."

GROUP EFFORT

OBSERVATIONS of modern-day dancers offer some tantalizing clues to the kinds of advantages dancing might have conferred in our evolutionary past. A notable feature of human dance is that we tend to do it together. As we feel and predict one another's movements, there is a physical and emotional give-and-take between individuals, whether they are tango partners or throngs of millennials rocking out to Bruno Mars.

This group capability represents what can be called social entrainment, and it confers what Émile Durkheim, who helped to create the field of sociology in the late 1800s, termed "collective effervescence," or the feeling of being part of something larger than oneself. That kind of social cohesion could be valuable for life-sustaining activities such as food gathering or predator avoidance.

Anthropologist Edward Hagen of Washington State Universi-

GETTY IMAGES (*6* and *7*); DAN KITWOOD *Getty Images* (*8*)

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ty Vancouver takes that idea a step further. He hypothesizes that music and dance might have evolved as a way for groups to appraise one another when seeking to form alliances that reached beyond the bonds of kinship. How well a group danced together, for instance, might give an indication of how well its members would perform as part of a larger coalition.

Greater social cohesion imparts physiological benefits as well. A 2010 study by scientists at the University of Oxford shows that synchronized physical activity driven by a unified goal—in this case, rowing in the university's boat club—significantly increased participants' pain thresholds compared with solo training. The authors attributed the increase to the release of endorphins, natural opioids in areas of the brain associated with mood. Robin I. M. Dunbar, an anthropologist and evolutionary psychologist at Oxford, argues that these endorphins strengthen social bonds when people engage in group musical activities as well.

ments have been recovered—provide hints of such activities having taken place among Upper Paleolithic peoples. Among them is Isturitz, a cave in the French Pyrenees, where bone pipes dating to 35,000 to 20,000 years ago were found.

"It's clear from the other archaeological evidence that lots of different groups were gathering at these sites at particular times of the year," says Oxford paleoanthropologist Iain Morley, author of the 2013 book *The Prehistory of Music: Human Evolution, Archaeology, and the Origins of Musicality*. "When we see that kind of big group activity in hunter-gatherer societies today, music and dance occur." Thus, Morley believes, humanity's ancestors were likely making music and dancing for tens of thousands of years—plenty of time for evolution to influence the outcome.

There is one absolute about this most elusive of art forms. Dancing is about communicating, whether it is between the participants themselves or the participants and the observers.

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"You could imagine two societies, one that didn't dance and one that did, and the one that did would have much stronger social bonds," says archaeologist Clive Gamble, a professor at the University of Southampton in England. In a competitive situation between the two, he says, the society that danced "would have an evolutionary advantage."

Given the dearth of direct evidence for the origins of dance, scientists in varying fields have turned to the behavior of today's few remaining hunter-gatherer societies for clues about our ancestral past. Their way of life probably offers the closest approximation that anthropologists have of what human societies were like before the widespread adoption of agriculture 10,000 years ago.

Evolutionary anthropologist Camilla Power of the University of East London studies the Hadza people of northern Tanzania, who typically live in "camps" of 20 to 30 people, in which men and women are social equals. Over the generations, dance has emotionally bound the Hadza and other groups, including the Bayaka people in central Africa and the San people in the Kalahari Desert, together in "shared fictions." Participants enact initiations, healing rituals and gender relationships, among other things, Power says. Among the Hadza, key dance rituals include feigned "sex wars" in which women taunt men and the men return the favor. "This dynamic is what underlies the egalitarianism," she says. Women consolidate their power, even playing male roles, goading the men to hunt in return for later "cuddles."

There is indirect evidence that large group dances have taken place for thousands of years. So-called aggregation sites—large, heavily trampled areas where prehistoric musical instru-

Dancers are, in essence, sharing a world of their own invention.

In doing so, they are also changing their brain. Clinicians and researchers alike have acknowledged the benefits of dance for people with movement disorders such as Parkinson's disease. Indeed, many who suffer from the tremors, stiffness and difficulty initiating movements that characterize Parkinson's can, by taking dance classes, regain some of their ability to entrain. As an added benefit, the classes help to form social bonds that may have been diminished by the disease.

Dance classes for people with Parkinson's do not, of course, aim to turn out the next Mora Godoy. But they offer their own transformations. This most ancient of human activities unites body and mind in ways we are only beginning to grasp. SA

Thea Singer is a Boston-based science journalist whose work has appeared in the *Washington Post*, *MIT Technology Review* and *Psychology Today*, among others. She is also author of *Stress Less* (Hudson Street Press, 2010).

MORE TO EXPLORE

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OUR DIGITAL DOUBLES

AI will serve our species, not control it

By Pedro Domingos

Illustration by Armando Veve

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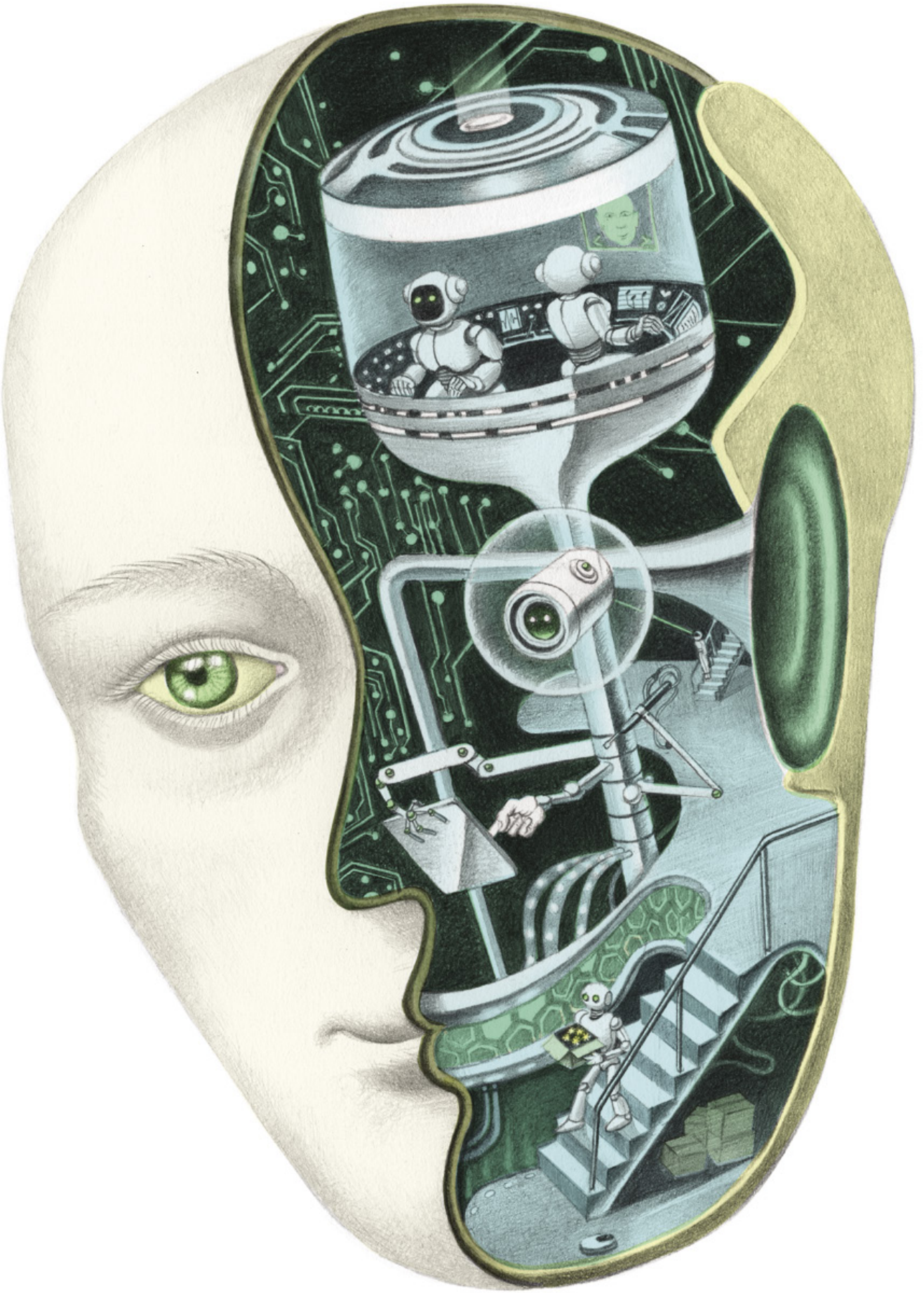

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HUMANS ARE THE ONLY ANIMALS THAT BUILD MACHINES. By doing so, we expand our capabilities beyond our biological limits. Tools turn our hands into more versatile appendages. Cars let us travel faster, and airplanes give us wings. Computers endow us with bigger brains and memory capacity, and smartphones orchestrate daily life. Now we are creating technology that can evolve on its own by encoding into it an ability to learn through data and effort. Will it ultimately supplant us? Or will it augment our abilities, enhancing our humanness in unprecedented ways?

IN BRIEF

The pursuit of artificial intelligence can be seen as part of human evolution. The next stage of automation will require the creation of a so-called master algorithm. It would integrate the five main ways that machines currently learn into a single, unified paradigm.

Technology is simply an extension of human capabilities. Machines do not have free will, only goals that we give to them. It is the misuse of the technology by people that we should be worried about, not a robot takeover.

A more plausible near-term scenario for AI is the proliferation of "digital doubles"—virtual models of ourselves that will interact with each other in countless simulations to help us make faster, more informed choices in our daily lives.

Machine learning started in the 1950s with the work of pioneering scientists such as Frank Rosenblatt, who built an electronic neuron that learned to recognize digits, and Arthur Samuel, whose checkers program learned by playing against itself until it could beat some humans. But it is only in the past decade that the field has truly taken off, giving us self-driving cars, virtual assistants that understand our commands (up to a point) and countless other applications.

Every year we invent thousands of new algorithms, which are sequences of instructions telling a computer what to do. The hallmark of learning machines, however, is that instead of programming them in detail, we give them general goals such as "learn to play checkers." Then, like humans, they improve with experience. These learning algorithms tend to fall into five main categories, each inspired by a different scientific field. Unsurprisingly, one way that machines learn is by mimicking natural selection, through evolutionary algorithms. In the Creative Machines Lab at Columbia University, primitive robots try to crawl or fly, and the specifications of those that perform best are periodically mixed and mutated to 3-D print the next generation. Starting with randomly assembled bots that can barely move, this process eventually produces creatures such as robot spiders and dragonflies after thousands or tens of thousands of generations.

But evolution is slow. Deep learning, currently the most popular machine-learning paradigm, takes inspiration from the brain. We start with a highly simplified mathematical model of how a neuron works and then build a network from thousands or millions of these units and let it learn by gradually strengthening the connections between neurons that fire together when looking at data. These neural networks can recognize faces, understand speech and translate languages with uncanny accuracy. Machine learning also draws on psychology. Like humans, these analogy-based algorithms solve new problems by finding similar ones in memory. This ability allows for the automation of customer support, as well as e-commerce sites that recommend products based on your tastes.

Machines may also learn by automating the scientific method. To induce a new hypothesis, symbolic learners invert the process of deduction: If I know that Socrates is human, what else do I need to infer that he is mortal? Knowing that humans are mortal would suffice, and this hypothesis can then be tested by checking if other humans in the data are also mortal. Eve, a biologist robot at the University of Manchester in England, has used this approach to discover a potential new malaria drug. Starting with data about the disease and basic knowledge of molecular biology, Eve formulated hypotheses about what drug compounds might work, designed experiments to test them, carried out the experiments in a robotic lab, revised or discarded the hypotheses, and repeated until it was satisfied.

Finally, learning can rely purely on mathematical principles, the most important of which is Bayes's theorem. The theorem says that we should assign initial probabilities to hypotheses based on our knowl-

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edge, then let the hypotheses that are consistent with the data become more probable and those that are not become less so. It then makes predictions by letting all the hypotheses vote, with the more probable ones carrying more weight. Bayesian learning machines can do some medical diagnoses more accurately than human doctors. They are also at the heart of many spam filters and of the system that Google uses to choose which ads to show you.

Each of these five kinds of machine learning has its strengths and weaknesses. Deep learning, for example, is good for perceptual problems such as vision and speech recognition but not for cognitive ones such as acquiring commonsense knowledge and reasoning. With symbolic learning, the reverse is true. Evolutionary algorithms are capable of solving harder problems than neural networks, but it can take a very long time to solve them. Analogical methods can learn from just a small number of instances but are liable to get confused when given too much information about each. Bayesian learning is most useful for dealing with small amounts of data but can be prohibitively expensive with big data.

These vexing trade-offs are why machine-learning researchers are working toward combining the best elements of all the paradigms. In the same way that a master key opens all locks, our goal is to create a so-called master algorithm—one that can learn everything that can be extracted from data, deriving all possible knowledge from it.

The challenge on us now is similar to the one faced by physicists: quantum mechanics is effective at describing the universe at the smallest scales and general relativity at the largest scales, but the two are incompatible and need to be reconciled. And in the same way that James Clerk Maxwell first unified light, electricity and magnetism before the Standard Model of particle physics could be developed, different research groups, including mine at the University of Washington, have proposed ways to unify two or more of the machine-learning paradigms. Because scientific progress is not linear and instead happens in fits and starts, it is difficult to predict when the full unification of the master algorithm might be complete. Regardless, achieving this goal will not usher in a new, dominant race of machines. Rather, it will accelerate human progress.

MACHINE TAKEOVER?

ONCE WE ATTAIN THE MASTER ALGORITHM and feed it the vast quantities of data each of us produce, artificial-intelligence systems will potentially be able to learn very accurate and detailed models of individual people: our tastes and habits, strengths and weaknesses, memories and aspirations, beliefs and personalities, the people and things we care about, and how we will respond in any given situation. That models of us could essentially predict the choices we will make is both exciting and disquieting.

Many worry that machines with these capabilities will use their newfound knowledge to take all our jobs, enslave us or even exterminate us. But that is unlikely to happen because they have no will of their own. Essentially all AI algorithms are driven by goals that we program, such as "find the shortest route from the hotel to the airport." What distinguishes these algorithms from ordinary ones is that they have a lot of flexibility in figuring out how to reach the goals we set for them rather than needing to execute a predefined series of steps. Even as they get better at the task with experience, the goals remain unchanged. Solutions that do not make progress toward the goal are automatically discarded. Plus, humans get to check that what the machines produce does indeed satisfy our objectives. We are also able to verify that the machines do not violate any of the constraints we put on them, such as "obey the rules of the road."

When we envision an AI, though, we tend to project onto it human qualities such as volition and consciousness. Most of us are also more familiar with humanlike AIs, such as home robots, than with the myriad other types that do their work behind the scenes. Hollywood compounds this perception by depicting robots and AIs as humans in disguise—an understandable tactic that makes for a more compelling story. Artificial intelligence is just the ability to solve hard problems—a task that does not require free will. It is no more likely to turn against us than your hand is to slap you. Like any other technology, AIs will always be extensions of us. The more powerful we can make them, the better.

What, then, might our AI-enabled future look like? Intelligent machines will indeed supplant many jobs, but the effects on society will likely be similar to previous forms of automation. Two hundred years ago the majority of Americans were farmers. Yet today machines have replaced almost all of them without causing massive unemployment. Doomsayers argue that this time is different because machines are replacing our brains, not just our brawn, leaving nothing for humans to do. But the day that AIs can carry out all the tasks we can is still very distant, if it ever comes. For the foreseeable future, AIs and humans will be good at different things. Machine learning's primary effect will be to greatly lower the cost of intelligence. This democratization will increase the variety of economically feasible uses of that intelligence, generating new jobs and transforming old ones to accomplish more with the same amount of human labor.

Then there is the "singularity" scenario, popularized by futurist Ray Kurzweil. It is one of ever accelerating technological progress: machines learn to make better machines, which in turn make even better ones, and so on. But we know that this cannot continue forever because the laws of physics place strict limits on how powerful even a quantum com-

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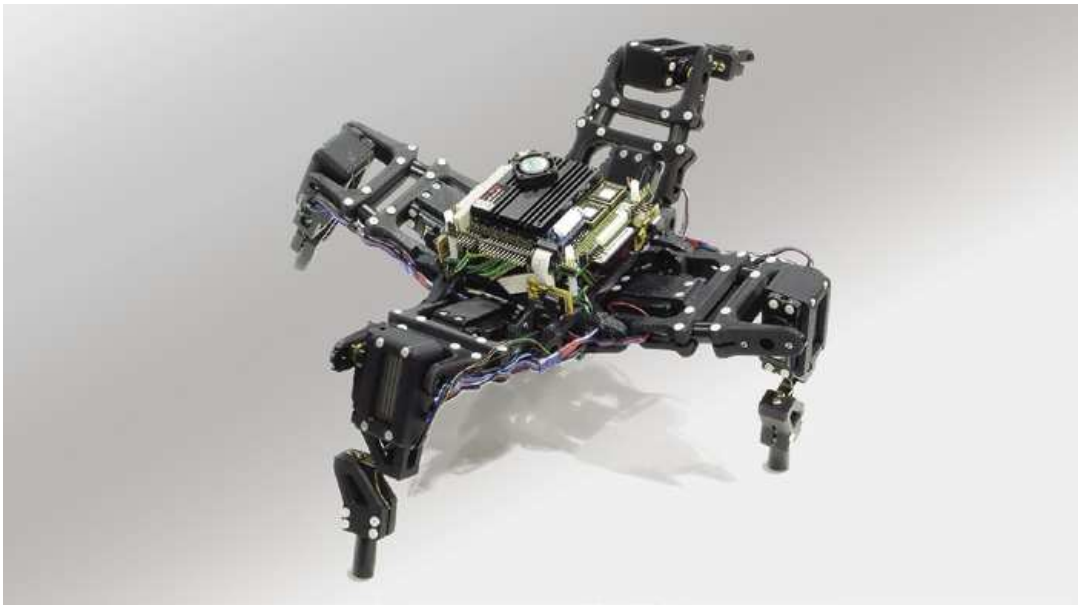

SMART BOT: This "sea star" robot uses evolutionary algorithms to learn how to simulate itself. These algorithms are one type of machine learning that could be unified with others into a "master algorithm," a singularly powerful human tool.

puter can be, and in some aspects, we are not far from hitting them. The progress of AI, like the progress of everything else, will eventually plateau.

Another vision popular among futurists is that computer models of us will become so good that they will be practically indistinguishable from the real thing. In this scenario, we could upload ourselves to the cloud and live on forever as pieces of software, free of the pesky constraints of the physical world. One problem with this scenario is that it may not be biologically feasible. To upload yourself, you would presumably need an accurate model of each of your neurons, complete with the memories they store. It would have to be captured so reliably that the model's predictions would not rapidly diverge from the behavior of the real neurons—a tall order indeed.

But even if this were a realistic option, would you really upload yourself if you had the chance? How could you know for sure that your model was not missing some essential part of you—or that it was conscious at all? What if a thief stole your identity in the most absolute and complete sense of the word? I believe that people will opt to hang on to their squishy, carbon-based selves—the "wetware," as computer scientists jokingly call it—for as long as they can and then call it quits.

CHERCHEZ L'HUMAIN

AI—MACHINE LEARNING IN PARTICULAR—is really just the continuation of human evolution. In *The Extended Phenotype,* Richard Dawkins shows how common it is for animals' genes to control the environment beyond their bodies, from cuckoo eggs to beaver dams. Technology is the extended phenotype of humans, and what we are building today is another layer of our technological exoskeleton. I think the most likely scenario for how humans will use AI is more fascinating than the usual speculations.

Within a decade each one of us will probably have a "digital double," an AI companion that will be even more indispensable than our smartphones are today. Your digital double will not need to physically move around with you; most likely it will live somewhere in the cloud, just as much of your data already does. We can see its beginnings in virtual assistants such as Siri, Alexa and Google Assistant. At the heart of your digital double will be a model of you, learned from all the data you have ever generated in your interactions with the digital world, from desktop computers and Web sites to wearable devices and sensors in the environment such as smart speakers, thermostats, cell-phone towers and video cameras.

The better our learning algorithms become and the more personal data we feed them, the more accurate our digital doubles will get. Once we have the master algorithm and then couple it with continuous capture of your sensorimotor stream via an augmented-reality headset and other personal sensors, your double will grow to know you better than your best friend.

The model and data will be maintained by a "data bank," not unlike a traditional bank that stores and invests your money. Many existing companies would surely like to provide that service for you. Google cofounder Sergey Brin has said that Google wants to be "the third half of your brain," but you probably would not want part of your brain to subsist by showing you ads. You might be better served by a new kind of company with fewer conflicts of interest or by a data union you form with like-minded people.

After all, the central worry about AI is not that it will spontaneously turn evil but that the humans who control it will misuse it (*cherchez l'humain,* as

VICTOR ZYKOV AND JOSH BONGARD

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the French might say—"look to the human"). So your data bank's first duty will be to ensure that your model is never used against your interests. Both you and the data bank must be vigilant about monitoring AI crime because this technology will empower bad actors as much as anyone. We will need AI police (the Turing police, as William Gibson called it in his 1984 book *Neuromancer*) to catch the AI criminals.

If you have the misfortune of living under an authoritarian regime, this scenario could usher in unprecedented dangers because it will allow the government to monitor and restrain you like never before. Given the speed at which machine learning is progressing and the predictive policing systems already in use, the *Minority Report* scenario—where people are preemptively arrested when they are about to commit a crime—no longer seems farfetched. Then there are the implications of inequality as the world adapts to the speed of life with digital doubles before all of us are able to afford one.

Our first duty, as individuals, will be not to become complacent and trust our digital doubles beyond their years. It is easy to forget that AIs are like autistic savants and will remain so for the foreseeable future. From the outside, AIs may seem objective, even perfect, but inside they are as flawed as we are or more, just in different ways. For example, AIs lack common sense and can easily make errors that a human never would, such as mistaking a person crossing the street for a windblown plastic bag. They are also liable to take our instructions too literally, giving us precisely what we asked for instead of what we actually wanted. (So think twice before telling your self-driving car to get you to the airport on time at all costs.)

Practically speaking, your digital double will be similar enough to you to take your place in all kinds of virtual interactions. Its job will not be to live your life for you but rather to make all the choices you do not have the time, patience or knowledge for. It will read every book on Amazon and recommend the few that you are most likely to want to read yourself. If you need a car, it will research the options and haggle with the car dealer's bots. If you are job hunting, it will interview itself for all the positions that fit your needs and then schedule live interviews for you for the most promising ones. If you get a cancer diagnosis, it will try all potential treatments and recommend the most effective ones. (It will be your ethical duty to use your digital double for the greater good by letting it take part in medical research, too.) And if you are seeking a romantic partner, your double will go on millions of virtual dates with all eligible doubles. The pairs that hit it off in cyberspace can then go on a date in real life.

Essentially your double will live out countless probable lives in cyberspace so that the single one you live in the physical world is likely to be the best version. Whether your simulated lives are somehow "real"

Your digital double will take your place in all kinds of virtual interactions.

and your cyberselves have a kind of consciousness (as portrayed in the plots of some *Black Mirror* episodes, for instance) are interesting philosophical questions.

Some people worry that this means that we are handing over control of our lives to computers. But it actually gives us more control, not less, because it allows us to make choices we could not before. Your model will also learn from the results of each virtual experience (Did you enjoy the date? Do you like your new job?) so that over time, it will become better at suggesting the things you would choose for yourself.

In fact, we are already accustomed to most of our decision-making taking place without our conscious intervention because that is what our brains do now. Your digital double will be like a greatly expanded subconscious, with one key difference: Whereas your subconscious lives alone inside your skull, your digital double will continuously interact with those of other people and organizations. Everyone's doubles will keep trying to learn models of one another, and they will form a society of models, living at computer speeds, branching out in all directions, figuring out what we would do if we were there.

Our machines will be our scouts, blazing a trail into the future for us as individuals and as a species. Where will they lead us? And where will we choose to go? SA

Pedro Domingos is a professor of computer science at the University of Washington and author of *The Master Algorithm* (Basic Books, 2015). A fellow of the Association for the Advancement of Artificial Intelligence, he lives near Seattle.

MORE TO EXPLORE

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STILL EVOLVING

(After All These Years)

For 30,000 years our species has been changing remarkably quickly. And we're not done yet

By John Hawks

IN BRIEF

Some scientists and science communicators have claimed that humans are no longer subject to natural selection and that human evolution has effectively ceased.

In fact, humans have evolved rapidly and remarkably in the past 30,000 years. Straight black hair, blue eyes and lactose tolerance are all examples of relatively recent traits.

Such rapid evolution has been possible for several reasons, including the switch from hunting and gathering to agrarian-based societies, which permitted human populations to grow much larger than before. The more people reproduce within a population, the higher the chance of new advantageous mutations.

Humans will undoubtedly continue to evolve into the future. Although it may seem that we are headed toward a cosmopolitan blend of human genes, future generations will likely be striking mosaics of our entire evolutionary past.

Illustration by Christian Northeast

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HUMANS ARE WILLFUL CREATURES. NO OTHER SPECIES ON THE PLANET has gained so much mastery over its own fate. We have neutralized countless threats that once killed us in the millions: we have learned to protect ourselves from the elements and predators in the wild; we have developed cures and treatments for many deadly diseases; we have transformed the small gardens of our agrarian ancestors into the vast fields of industrial agriculture; and we have dramatically increased our chances of bearing healthy children despite all the usual difficulties.

Many people argue that our technological advancement—our ability to defy and control nature—has made humans exempt from natural selection and that human evolution has effectively ceased. There is no "survival of the fittest," the argument goes, if just about everyone survives into old age. This notion is more than just a stray thought in the public consciousness. Professional scientists such as Steve Jones of University College London and respected science communicators such as David Attenborough have also declared that human evolution is over.

But it is not. We have evolved in our recent past, and we will continue to do so as long as we are around. If we take the more than seven million years since humans split from our last common ancestor with chimpanzees and convert it to a 24-hour day, the past 30,000 years would take about a mere six minutes. Yet much has unfolded during this last chapter of our evolution: vast migrations into new environments, dramatic changes in diet and a more than 1,000-fold increase in global population. All those new people added many unique mutations to the total population. The result was a pulse of rapid natural selection. Human evolution is not stopping. If anything, it is accelerating.

AN ANTHROPOLOGICAL LEGACY

SKELETONS OF ANCIENT PEOPLE have long suggested that humans evolved certain traits swiftly and recently. About 11,000 years ago, as people started to transition from hunting and gathering to farming and cooking, human anatomy changed. Ten thousand years ago, for example, people's teeth averaged more than 10 percent larger in Europe, Asia and North Africa than today. When our ancestors started to eat softer cooked foods that required less chewing, their teeth and jaws shrank, bit by bit, each generation.

Although anthropologists have known about such traits for decades, only in the past dozen years has it become clear just how new they really are. Studies of human genomes have made the recent targets of selection highly visible to us. It turns out, for example, that descendants of farmers are much more likely to have a greater production of salivary amylase, a key enzyme that breaks down starches in food. Most people alive today have several copies of the gene that codes for amylase, *AMY1*. Modern hunter-gatherers—such as the Datooga in Tanzania—tend to have far fewer copies than people whose ancestors came from farming populations, whether they live in Africa, Asia or the Americas. Getting a jump on starch processing at the point of entry seems to have been an advantage for ancient farmers wherever they adopted starchy grains.

Another dietary adaptation is one of the best-studied examples of recent human evolution: lactose tolerance. Nearly everyone in the world is born with the ability to produce the enzyme lactase, which breaks down the milk sugar lactose and makes it easier to extract energy from milk—essential for the survival of a suckling child. Most people lose this ability by adulthood. At least five different times in our recent evolutionary past, as people started to discover dairy, a genetic mutation arose to lengthen the activity of the lactase gene. Three of the mutations originated in different parts of sub-Saharan Africa, where there is a long history of cattle herding. Another one of the five genetic

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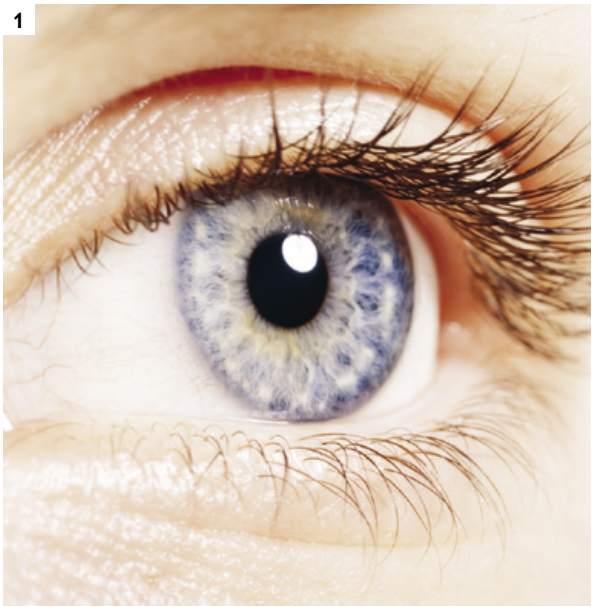
Recent Traits

Many commonplace features of human biology are relatively new (*1–3*). Blue eyes, straight, thick black hair, the ability to digest milk in adulthood and some mutations that lightened skin all emerged in the past 30,000 years.

1



2

3

ANTHONY LEE *Getty Images (1)*; ANDREAS KUEHN *Getty Images (2)*; DAITOZEN *Getty Images (3)*

tweaks is common in Arabia and seems to have sprung up in ancient populations of camel and goat herders.

The fifth and most common variant of the mutation that keeps the lactase gene turned on in adulthood is found today in human populations stretching from Ireland to India, with its highest frequencies across northern Europe. The mutation originated in a single individual 7,500 years ago (give or take a few thousand years). In 2011 scientists analyzed DNA recovered from Ötzi the Iceman, who was naturally mummified about 5,500 years ago in northern Italy. He did not have the lactose-tolerance mutation, a hint that it had not yet become common in this region thousands of years after its initial origin. In following years, researchers sequenced DNA extracted from the skeletons of farmers who lived in Europe more than 5,000 years ago. None carried the lactase mutation. Yet in the same region today, the lactase-persistence mutation occurs in hundreds of millions of people—more than 75 percent of the gene pool. This is not a paradox but the mathematical expectation of natural selection. A new mutation under selection grows exponentially, taking many generations to become common enough to notice in a population. But once it becomes common, its continued growth is very rapid and ultimately dominates.

THE SHALLOWNESS OF RACES

WHAT IS PERHAPS MOST EXTRAORDINARY about our recent evolution is how many common physical features are completely new to human anatomy. The thick, straight black hair shared by most East Asians, for example, arose only within the past 30,000 years, thanks to a mutation in a gene called *EDAR,* which is crucial for orchestrating the early development of skin, hair, teeth and nails. That genetic variant traveled with early colonizers of the Americas, all of whom share an evolutionary past with East Asians.

In fact, the overall evolutionary history of human skin, hair and eye pigmentation is surprisingly shallow. In the earliest stages of our evolution, all our ancestors had dark skin, hair and eyes. Since this initial state, dozens of genetic changes have lightened these features to some extent. A few of these changes are ancient variations present within Africa but more common elsewhere in the world. Most are new mutations that have emerged in one population or another: a change in a gene named *TYRP1,* for instance, that makes certain Solomon Islanders blond; the *HERC2* mutation that results in blue eyes; changes to *MC1R* that causes red hairs to sprout instead of black ones; and a mutation in the *SLC24A5* gene that lightens skin color and that is now found in up to 95 percent of Europeans. As in the case of lactase, ancient DNA is giving clear information about the antiquity of such mutations. Blue eyes seem to have appeared in people who lived more than 9,000 years ago, but the massive change to *SLC24A5* is not found in the DNA of ancient skeletons from the same time period. Skin, hair and eye color evolved with stunning speed.

Variations in pigmentation are some of the most obvious differences between the races and, in some ways, the easiest to study. Scientists have also investigated much odder and less evident features of human anatomy. Consider the variations of earwax. Most people in the world today have sticky earwax. In contrast, many East Asians have dry, flaky earwax that does not stick together. Anthropologists have known about this variation for more than 100 years, but geneticists did not uncover the cause until recently. Dry earwax results from a relatively new mutation to a gene called *ABCC11.* Only 30,000 to 20,000 years old, the mutation also affects the apocrine glands, which produce sweat. If you have stinky armpits and sticky earwax, chances are you have the original version of *ABCC11.* If you have dry earwax and a little less need for deodorant, you probably have the newer mutation.

A few thousand years before dry earwax first appeared

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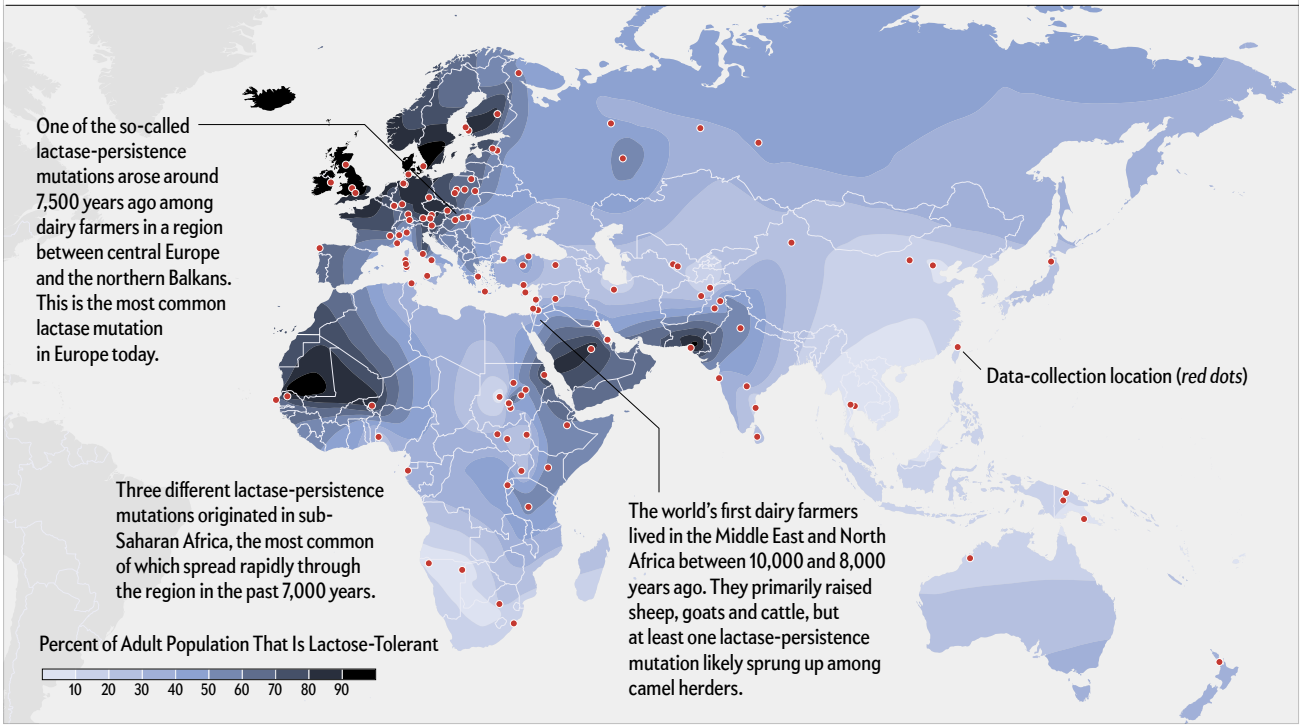
The Milk Mutation

Enjoying dairy in adulthood is a privilege that emerged relatively recently in our evolutionary history. We depend on the enzyme lactase to break down lactose, the sugar found in milk, but the human body usually stops producing lactase after adolescence. In fact, most of the world's adults are lactose-intolerant. Within the past 10,000 years, however, different populations of dairy farmers independently evolved genetic mutations that kept lactase active throughout life (lactase persistence). Scientists have identified several such mutations, but there are likely more. Collectively, all these adaptations explain the prevalence of lactose tolerance seen around the world today.


One of the so-called lactase-persistence mutations arose around 7,500 years ago among dairy farmers in a region between central Europe and the northern Balkans. This is the most common lactase mutation in Europe today.
Data-collection location (red dots)
Three different lactase-persistence mutations originated in sub-Saharan Africa, the most common of which spread rapidly through the region in the past 7,000 years.
The world's first dairy farmers lived in the Middle East and North Africa between 10,000 and 8,000 years ago. They primarily raised sheep, goats and cattle, but at least one lactase-persistence mutation likely sprung up among camel herders.
Percent of Adult Population That Is Lactose-Tolerant
10 20 30 40 50 60 70 80 90

among East Asians, another seemingly simple mutation started saving millions of Africans from a deadly disease. A gene called *DARC* produces a starchy molecule on the surface of red blood cells that mops up excess immune system molecules known as chemokines from the blood. About 45,000 years ago a mutation in *DARC* conferred remarkable resistance to *Plasmodium vivax,* one of the two most prevalent malaria parasites infecting humans today. The *vivax* parasites enter red blood cells through the *DARC* molecule encoded by the gene, so hindering the expression of *DARC* keeps the pathogens at bay. The absence of *DARC* also increased the amount of inflammation-causing chemokines circulating in the blood, which has in turn been linked to an increase in prostate cancer rates in African-American men. Yet on the whole, the mutation was so successful that 95 percent of people living below the Sahara now have it, whereas only 5 percent of Europeans and Asians do.

THE POWER OF RANDOM

WE ARE ACCUSTOMED TO THINKING about evolution as a process of "good" genes replacing "bad" ones, but the most recent phase of human adaptation is a testament to the power of randomness in evolution. Beneficial mutations do not automatically persist. It all depends on timing and on population size.

I first learned this lesson from anthropologist Frank Livingstone. The beginning of my training coincided with the end of his long career, during which he investigated the genetic basis for malaria resistance. More than 3,000 years ago in Africa and India, a mutation arose in the gene coding the oxygen-transporting blood cell molecule known as hemoglobin. When people inherited two copies of this mutation—dubbed hemoglobin S—they developed sickle cell anemia, a disease in which unusually shaped blood cells clog vessels. Red cells are normally supple and flexible enough to squeeze through tiny capillaries, but the mutant blood cells were rigid and deformed into the characteristic "sickle" shape. As it turns out, changing the shape of red blood cells also thwarted the ability of the malaria parasite to infect those cells.

Another mutation that interested Livingstone was hemoglobin E. Common in Southeast Asia today, hemoglobin E confers substantial malaria resistance without the severe side effects of hemoglobin S. "Hemoglobin E seems like it would be a lot better to have than hemoglobin S," I said in class one day. "Why didn't they get E in Africa?"

"It didn't happen there," Livingstone said.

His reply stunned me. I had supposed natural selection to be the most powerful force in evolution's arsenal. Humans had

SOURCE: GLOBAL LACTASE PERSISTENCE ASSOCIATION DATABASE

Map by XNR Productions

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lived with deadly *falciparum* malaria for thousands of years in Africa. Surely natural selection would have weeded out less helpful mutations and hit on the most successful one.

Livingstone went on to show how the previous existence of hemoglobin S in a population made it harder for hemoglobin E to invade. Malaria rips through a population full of only normal hemoglobin carriers, and a new mutation that provides a slight advantage can quickly become more common. Yet a population already supplied with the protective hemoglobin S mutation will have a lower mortality risk. Sickle cell carriers still face formidable risks, but hemoglobin E is less of a *relative* advantage in a population that already has this imperfect form of malaria resistance. Perversely, what matters is not only the luck of having the mutation but also *when* the mutation happens. A partial adaptation with bad side effects can win, at least over the few thousand years humans have been adapting to malaria.

Ever since humans first began battling malaria, scores of different genetic changes emerged that increased immunity to the disease, different ones in different places. Each started as a serendipitous mutation that managed to persist in a local population despite being very rare at first. Any one of those mutations was, individually, unlikely to last long enough to become established, but the huge and rapidly increasing population size of our ancestors gave them many more rolls of the dice. As human populations have spread into new parts of the world and grown larger, they have rapidly adapted to their new homes precisely because those populations were so big.

OUR EVOLUTIONARY FUTURE

HUMAN POPULATIONS CONTINUE to evolve today. Unlike the distant past, where we must infer the action of selection from its long-term effects on genes, today scientists can watch human evolution in action, often by studying trends in health and reproduction. Even as medical technology, sanitation and vaccines have greatly extended life spans, birth rates in many populations still vacillate.

In sub-Saharan Africa, women who have a certain variant of a gene called *FLT1* and who are pregnant in the malarial season are slightly more likely to bear children than are pregnant women who lack the variant because the possessors have a lower risk that the placenta will be infected by malaria parasites. We do not yet understand how this gene reduces the risk of placental malaria, but the effect is profound and measurable.

Stephen Stearns of Yale University and his colleagues have examined years of records from long-term public health studies to see which traits may correlate with reproduction rates today. During the past 60 years, relatively short and heavy women in the U.S. who have low cholesterol counts had slightly more children on average than women who have the opposite traits. Why these traits have been related to family size is not yet clear.

Public health studies, such as U.K. Biobank, track the genotypes and lifetime health of hundreds of thousands of people. Such studies are being undertaken because the interactions of genes are complicated, and we need to examine thousands of outcomes to understand which genetic changes underlie human health. Tracing the ancestry of human mutations gives us tremendous power to observe evolution over hundreds of generations but can obscure the complex interactions of environment, survival and fertility that unfolded in the past. We see the long-term winners, such as lactase persistence, but may miss the short-term dynamics. Human populations are about to become the most intensively observed long-term experiment in evolutionary biology.

INSTEAD OF A FEATURELESS MASS OF CAFÉ-AU-LAIT-COLORED CLONES, WE ARE ALREADY STARTING TO SEE A GLORIOUS RIOT OF VARIATIONS—DARK-SKINNED, FRECKLED BLONDES AND STRIKING COMBINATIONS OF GREEN EYES AND OLIVE SKIN.

What will the future of human evolution look like? Across the past few thousand years, human evolution has taken a distinctive path in different populations yet has maintained surprising commonality. New adaptive mutations may have elbowed their way into human populations, but they have not muscled out the old versions of genes. Instead the old, "ancestral" versions of genes mostly have remained with us. Meanwhile millions of people are moving between nations every year, leading to an unprecedented rate of genetic exchanges and mixture.

With such a high rate of genetic mixing, it may seem reasonable to expect that additive traits—for example, pigmentation, where many different genes have independent effects on skin color—will become ever more blended in future human populations. Could we be looking at a human future where we are a homogeneous slurry instead of a colorful stew of variability?

The answer is no. Many of the traits that differ between human populations are not additive. Even pigmentation is hardly so simple, as is readily seen in mixed populations in the U.S., Mexico and Brazil. Instead of a featureless mass of café-au-lait-colored clones, we are already starting to see a glorious riot of variations—dark-skinned, freckled blondes and striking combinations of green eyes and olive skin. Each of our descendants will be a living mosaic of human history. SA

John Hawks is an anthropologist and an expert on human evolution at the University of Wisconsin–Madison.

MORE TO EXPLORE

Are Human Beings Still Evolving? It Would Seem That Evolution Is Impossible Now That the Ability to Reproduce Is Essentially Universally Available. Are We Nevertheless Changing as a Species? Meredith F. Small; Ask the Experts, ScientificAmerican.com, October 21, 1999.

African Adaptation to Digesting Milk Is "Strongest Signal of Selection Ever." Nikhil Swaminathan; ScientificAmerican.com, December 11, 2006.

Why We "Got Milk." Andrew Curry; ScientificAmerican.com, July 31, 2013.

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Starship Humanity

How will future generations make the voyage from our earthly home to the planets and beyond—and what will that mean for our species?

By Cameron M. Smith

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Illustration by Tavis Coburn

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WHEN SPACE SHUTTLE *ATLANTIS* ROLLED TO A STOP IN 2011, it did not mark, as some worried, the end of human spaceflight. Rather, as the extinction of the dinosaurs allowed early mammals to flourish, retiring the shuttle signaled the opening of far grander opportunities for space exploration. Led by dozens of ambitious private companies, we are entering the early stages of the dispersal of Earth life into the solar system at large. The European Space Agency has revealed plans for a lunar habitat, and a Mars settlement is the stated goal of Elon Musk's SpaceX company. The international research team Icarus Interstellar is taking this century to design propulsion technologies and great starships, ultimately to send an entire culture to a distant exoplanet. The human settlement of space is beginning now.

But technology is not enough. If space settlement is to succeed in the long run, we must consider biology and culture as carefully as engineering. Space settlement cannot be about rockets and robots alone—it will have to embrace bodies, people, families, communities and cultures. We must begin to build an anthropology of space settlement to grapple with the fuzzy, messy, dynamic and often infuriating world of human bioculturral adaptation. And we must plan this new venture while remembering the clearest fact of all regarding living things: they change through time, by evolution.

Three main concepts shape current thought about space settlement. First is the colonization of Mars. Widely publicized by the peppery space engineer and president of the Mars Society, Robert Zubrin, Martian colonies would be self-sufficient, using local resources to generate water and oxygen as well as to make construction materials. Next is the concept of free-floating colonies—enormous habitats built from lunar or asteroid metals. Popularized by physicist Gerard K. O'Neill in the 1970s, these would house thousands of people, could rotate to provide an Earth-like gravity (as beautifully envisioned in the 1968 film *2001: A Space Odyssey*), and could either orbit Earth or hang motionless at so-called Lagrangian points, spots where an object's orbital motion balances the gravitational pull of the sun, moon and Earth. Finally, we might also consider the concept of the Space Ark, a giant craft carrying thousands of space colonists on a one-way, multigenerational voyage far from Earth. I have been working with the nonprofit foundation Icarus Interstellar to design just such a mission.

Each of these approaches has its merits, and I think they are all technologically inevitable. But we must never confuse space colonization with the conquest of space. Successfully settling space beyond Earth will be an enormous challenge. Space is vast and unforgiving. When humanity begins to make its home in space, it is we who will change.

THE PIONEERS

WHO WILL BE THE SPACE COLONISTS? Here we must ditch the old concept of crew selection and the comically diabolical tests of chisel-chinned space heroes depicted in *The Right Stuff*. Space colonists will be ordinary families and communities who will not be on a mission but who are intending to live out their lifetimes. We will need a few Captain Picards, although most early colonists will probably be farmers and construction workers.

Still, early colonists will have to be genetically healthy. In smallish populations, individuals carrying genetic maladies could threaten the future in ways that do not play out in a population of billions. In a Space Ark, the biological fate of the colony is strongly conditioned by the genetic constitution of the founding population—if just a few travelers carry the genes for inherited disease, these genes will spread much more thoroughly.

We now know the details of hundreds of genes that cause disorders, from cancers to deafness. (Researchers can already screen for thousands of such traits prenatally and during a person's lifetime.) A genetic screening program seems clear—if you are carrying certain genes, you remain Earth-bound—but life is not so simple. Many maladies are polygenic—that is, the result of complex interactions among myriad genes. And even though one might carry the gene or genes for a certain disorder, environmental factors encountered during the course of life can determine whether or not those genes are activated in a healthy or unhealthy way.

For example, the human *ATRX* gene helps to regulate processes related to oxygen transportation. But *ATRX* activity can be altered by environmental influences as diverse as nutrient intake or a person's state of mind. When *ATRX* function is significantly modified, oxygen transport is impeded, resulting in seizures, mental disabilities and stunted growth. Thus, one cannot simply screen out people carrying *ATRX:* everyone has it. In some peo-

IN BRIEF

A space mission that isolates people away from Earth for extremely long periods—for instance, a Mars colony or a multigenerational voyage to a nearby star—will inevitably lead to the evolution of new cultural and physiological traits.

Long-distance spaceships will be home to unique environmental hazards such as increased radiation and lower ambient pressures. These influences will most severely affect the most fragile stages of life—in the womb and just after birth.

Mission planners will have to carefully select the "crew" of space travelers. Their goal: a genetically healthy population but one diverse enough to withstand the occasional pandemic and thrive in profoundly new environments.

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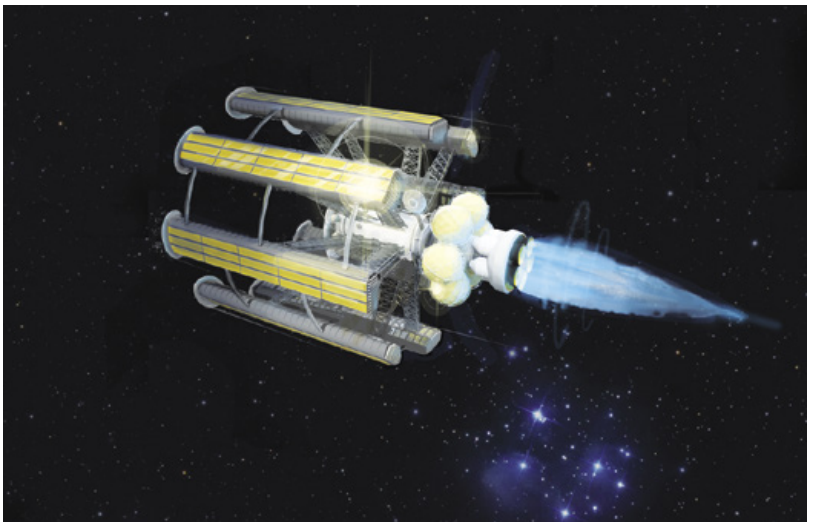
ple, though, based on poorly understood environmental factors, *ATRX* will go haywire. Can we deselect someone for space colonization for something that *might* happen? After reviewing this issue over the past few years, I've concluded that unless space-settling populations were to be very small, on the order of just a few hundred individuals, there would be no real need of genetic screening.

Complicating matters, we must also ensure broad genetic diversity of the gene pool. If all members of a population are genetically identical, a single sweep of disease could wipe everyone out. (This consideration demolishes the concept of a genetically engineered superrace of space travelers, as depicted in the 1997 film *Gattaca*.)

Once screened, what should be the population of space colonies? In a Mars colony, populations can grow and expand into new territory. But in a Space Ark, the population will be relatively low, and inbreeding becomes a concern. For example, in a study of Amish, Indian, Swedish and Utah populations, infant mortality was roughly double when matings occurred between first cousins than when they occurred between unrelated people.



SHIP SHAPE: Interstellar spacecraft will have to carry thousands of people, plus the plants and animals needed to support them.

To avoid these issues, we will have to consider the minimum population needed to maintain a healthy gene pool. Our minimum viable population has been much debated, but several anthropologists have suggested a figure of about 500. Because small populations are always at greater risk of collapse, in the past I have suggested founding populations of about 2,000 in a spacecraft that gives this population ample room to grow. For humans away from Earth, safety will indeed be found in numbers. (Even interstellar voyages will focus on reaching another solar system and inhabiting its planets, where populations can grow again.) Over the past year, my colleagues and I have used computer models and statistical investigation to verify these numbers. We found that multiple village-size populations, perhaps 1,000 or so each, could serve as a basis for even multiple-century interstellar voyages. Ten of these flying in parallel, connected so that people could visit other "towns" for friendship and to find mates, might be ideal.

We will also have to carefully consider the colonists' demographic structure—the age and sex of colonial populations. Simulations by my colleague William Gardner-O'Kearney show that over a few centuries, populations that begin with certain ratios of young to old and males to females persist better than others.

Early colonial populations, then, should be individually healthy and collectively diverse to give future populations the best chance of having genes on hand that might be adaptive in new environments. But we cannot control everything. At some point we will have to roll the genetic dice—which we already do every time we choose to have children on Earth—and set out from our cradle planet.

SPACE-BASED SELECTION

NO MATTER HOW CAREFULLY we prepare our colonial populations, life off planet Earth, at least at first, will be more dangerous and perhaps shorter than life here. Away from Earth, people will be exposed to forces of natural selection that we have technically all but removed from modern life. Little of this selection will play out in the dramatic ways we might expect from science-fiction movies, which tend to focus on the lives of adults. Instead it will occur during critical periods of tissue development in embryos and infants, when life is most delicate.

How could such selection play out? As one example, consider that the human body has evolved close to sea level under an atmospheric pressure of roughly 15 pounds per square inch (psi) for the past several million years, breathing a mix of roughly 80 percent nitrogen and 20 percent oxygen. Yet space travel requires pressurized habitats that grow more expensive and laborious to build the more pressure they need to hold. To ease the engineering requirements, atmospheric pressure in any off-Earth structure will be lower than on Earth.

Fair enough—*Apollo* astronauts survived just fine at 5 psi—but if you lower atmospheric pressure, you must increase oxygen as a percentage of what you are breathing. (Those same astronauts breathed 100 percent oxygen on their lunar voyages.)

Unfortunately, lower atmospheric pressure and elevated oxygen levels both interfere in vertebrate embryo development. Miscarriages and infant mortality will rise—at least for a time. Inevitably, selection will preserve the genes suitable for extraterrestrial conditions and remove those that are less suitable.

Infectious disease—to which small, dense populations such as space colonies are particularly vulnerable—will return as a significant concern, imposing new selection pressures as well. However careful we are with immunization and quarantine, plagues will eventually sweep through colonies, resulting in selection for people more capable of surviving the disease and selection against those less capable.

Finally, we must remember that we bring with us thousands of domesticates—plants and animals for food and materials—and that selective pressures will act on them as well. Ditto the millions of microbial species that ride on and in human bodies—invisible genetic hitchhikers that are critical to our health.

COURTESY OF STEVE SUMMERFORD *Icarus Interstellar–Project Hyperion*

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Based on a few calculations, I think it is reasonable that within five 30-year generations—about 150 years—such changes will be apparent in the extraterrestrial human body.

Exactly what biological adaptations evolve will depend heavily on the atmospheric and chemical environments of the habitats we build. We can control these to a large extent. Yet we cannot easily control two other important factors that will shape humanity in space: gravity and radiation.

Mars colonists will feel just a third of Earth's gravity. Over generations, without Earth's gravity, a heavier build will probably be replaced with a lighter, lither Martian stature. In Space Ark and other free-floating scenarios, gravitation might remain about Earth normal, so Earth-normal statures might persist.

SPACE LIFE: We cannot predict how the culture of a space outpost will change over hundreds of years—only that it will.

Radiation causes mutations, and any space colony will be unlikely to provide the protection from radiation that Earth's atmosphere and magnetic field provide. Will increased mutations create physical errors—repeated parts like an extra finger or malformed parts like a cleft palate? Certainly, but we cannot know what kind. The only thing we can predict with confidence is selection for increased resistance to radiation damage. Some people have better and more active DNA-repair mechanisms than others, and they will be more likely to pass their genes on.

Could more efficient DNA-repair mechanisms have any visible correlate—such as, say, a particular hair color? Again, we do not know. But it is also possible for beneficial genetics to spread when they have no such visible correlates. Among Hutterites of South Dakota, who interbreed among a relatively small number of small communities, anthropologists have found that people appear to be strongly influenced in their mate choice by body aroma—and the better the person's immune system, fascinatingly, the better the aroma.

On a moderate, five-generation timescale, then, human bodies will be subtly reshaped by their environment. We will see the origins of adaptations on the order of those of the natives of the high Andes and Tibet, where a more efficient oxygen-transport physiology has evolved, resulting in broader and deeper chests. Each alteration is a compromise, however, and these high-altitude populations also sustain higher infant mortality when giving birth at altitude. One cultural adaptation to this biological change has been for mothers to descend to oxygen-richer altitudes to deliver children. We can expect similar biocultural shifts off of Earth, and we should plan for the most likely of them. For example, on Mars, birthing mothers might shuttle to an orbiting station where delivery could happen in a rotating, 1-g facility with a more Earth-normal atmosphere, but I bet that eventually they would not bother and that distinctive Martian human characteristics would evolve.

A SPACE-BASED CULTURE

CULTURAL CHANGE will be more apparent than biological change on a 150-year time span. Studies of human migrations have taught us that while migrating peoples tend to carry on some traditions to maintain identity, they also devise novel traditions and customs as needed in new environments. For example, the Scandinavians who first colonized Iceland after A.D. 800 continued to worship Norse gods and speak the Viking language but quickly developed a distinctive cuisine—heavy on meat (whereas rye and oats were grown in Scandinavia) and on preserved foods to survive the harsh winters—as they explored the resources of an unknown land.

On Mars, this acculturation will play out in innumerable ways. There, in low-pressure, oxygen-rich atmospheres contained in unique architectural materials and arrangements, sound might propagate differently—even if subtly—perhaps affecting pronunciation and even the pacing of speech, resulting in novel accents and dialects. The lighter gravity could influence body language, an important element of human communication, and would influence performance arts of all kinds. Cultural divergence occurs as just such small, innumerable differences accumulate.

More profound cultural change could occur in Space Ark scenarios, where life would have less to do with Earth at each moment that the starship speeds away. Here basic concepts of space and time could well be transformed rather quickly. For example, how long would Space Ark cultures use Earth timekeeping? Without Earth's days and nights and years, civilizations might invent a base-10 timekeeping scale. Or they might decide to count time down until a distant solar system is reached rather than up from some event in the past (such as the departure from an Earth to which they will never return).

LONG-TERM GENETIC CHANGE

SIGNIFICANT GENETIC CHANGE occurs when new genes become widespread in a population. An example from prehistory is the spread of genes that resulted in lactose tolerance in adults, which appeared independently in both Africa and Europe not long after the domestication of cattle. This genetic equipment allowed

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more energy to be derived from cattle, and in these populations, it quickly became nearly universal, or "fixed."

Although we cannot predict which mutations will arise, population genetics enables us to estimate how long it would take mutations to become fixed in the genome of space-based explorers. My calculations—based on model Mars populations of 2,000 people of certain age and sex structures—indicate that it could occur in just a few generations and certainly within 300 years; we can expect subtle original off-Earth physical characteristics in human populations on this timescale. These changes will be on the order of the broad geographical variation we see in humans today—variation in statures, skin colors, hair textures and other features.

On Mars, there might be further, internal divergence as some populations elect to live most of their lives sheltered in underground habitats, while others prefer to take the increased radiation risks to live in surface habitats offering greater mobility. In the limited-population, closed-system Space Ark scenario, gene fixation could happen much more rapidly, perhaps driving a greater uniformity than on Mars.

Whereas there will be some biological change, long-term cultural change will be more profound. Consider that in the three centuries from the early 1600s to the early 1900s, the English language changed so much that comprehending 17th-century English texts today requires special training. Three centuries hence, the language spoken on a Space Ark might be profoundly different.

Larger-scale cultural change is also quite likely. Exactly what divides one culture from another is a topic of tremendous debate in anthropology, but I believe that anthropologist Roy Rappaport made the distinction clear. Different cultures have different "ultimate sacred postulates"—core concepts, usually unquestionable and unquestioned, ingrained by tradition and ritual, that shape a population's essential philosophical and moral codes. For Christianity, for example, one such postulate is that "In the beginning, God created the heaven and the Earth." How long it will take for such foundation beliefs to change off of Earth—and in what direction—is impossible to say, but several centuries is certainly enough time to allow new cultures to arise.

THE EVOLUTION OF *HOMO EXTRATERRESTRIALIS*

WHEN WILL WE SEE even more fundamental biological change—that is, speciation? Small populations can change quickly, as evidenced by the unusually large mice that roam the Faroe Islands 1,200 years after Viking ships dropped off ordinary house mice. But anatomically modern humans have gone more than 100,000 years—migrating from Africa into a wide variety of environments, from desert to open ocean—apparently without biological speciation. (Our nearest hominin relatives, such as the cold-adapted Neandertals and the apparently miniaturized "hobbit" humans of the island of Flores in the western Pacific, split from our common ancestor substantially earlier.) This is largely because we use culture and technology to adapt more than biology alone. It would take, then, significant natural and cultural selection to reshape extraterrestrial humans to such a degree that they could no longer productively mate with earthlings.

Unless, of course, humans devise their own speciation. It seems inevitable that off-Earthers will eventually harness the staggering power of DNA to tailor their own bodies for many conditions. Our distant descendants on Mars might biologically engineer gill-like structures to split the oxygen from atmospheric carbon dioxide—a process NASA is currently investigating—and skin tissues that could endure low surface pressure. They might tailor themselves into a new species, *Homo extraterrestrialis,* by conscious choice.

WHERE TO BEGIN?

HUMAN SPACE COLONIZATION will require plenty of engineering and technical advances. We must also improve our understanding of how human biology and culture adapt to new conditions and use that knowledge to help space colonization succeed. I suggest beginning immediately with three courses of action.

First, we must abandon the technocrat's essential revulsion of humanity and begin procreating off of Earth, giving birth there and raising children there, to understand critical issues of human reproduction, development, and growth in new radiation, pressure, atmospheric and gravity environments. Bureaucrats will recoil at the risks involved—children exposed to risk beyond that of a bicycle-helmeted, First World suburbanite!—but concerns will diminish as space access is privatized. Still, at times the adaptation to space will be painful—but so is birth.

Second, we must experiment with growing and maintaining the health of domesticated species off of Earth. We are going nowhere without our microbes, plants and other animals.

And to promote these first two goals, an X-Prize should be awarded for the first functional, livable human habitat off of Earth: not a sterile orbiting laboratory (as important as those are) but a home where people can grow plants, raise animals and even have children. Many would shudder at the prospect of staying in such a place, but at the same time, there will be no shortage of volunteers.

Finally, we must reengage the proactive approach that has made human survival possible up to the present and use that capacity to shape our own evolution beyond our home planet. We must be immensely bolder than our bureaucracies. Failing that, in time we will become extinct, like everything else on Earth. As H. G. Wells wrote about the human future in 1936, it is "all the universe or nothing." SA

Cameron M. Smith, Ph.D., teaches human evolution at Portland State University. He has written about evolution in his books *The Fact of Evolution* (Prometheus, 2011) and *Emigrating Beyond Earth* (Springer Praxis, 2012). His new book is a technical foundation for space settlement: *Principles of Space Anthropology: Establishing a Science of Human Space Settlement* (Springer, 2019).

MORE TO EXPLORE

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Cranes (here *Grus japonensis*) form long-term pair bonds that may last the birds' lifetime.

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Monogamy May Be Written in Our Genes

In animal studies, a set of 42 genes involved in neural development, learning and memory, and cognition seems to be associated with monogamy

By Karen Hopkin

What makes one species pair off, and members of a closely related species play the field? The answer may lie in their genes.

Researchers at the University of Texas at Austin were interested in how complex characteristics—such as monogamy—arise during evolution. "We chose to investigate this question using monogamous mating systems because animals with monogamous mating systems are available in all the different vertebrate clades," says Rebecca Young, a research associate and evolutionary biologist, who led the study. "And we were able to find species that had independently evolved monogamy in each of these lineages." This sampler of species provided the researchers with the evolutionary equivalent of a bird's-eye view of the behavior.

"We decided early on that we didn't just want to study a particular group of animals, like mice or fish, for example, or a particular group of birds, and compare between monogamy or nonmonogamy there," says Young's colleague Hans Hofmann, professor of integrative biology. "Instead we took a very broad look across vertebrates—across 450 million years of evolution—when these fish and birds and frogs and us shared the last common ancestor."

The researchers chose five pairs of species, and they looked to see if they could spot a signature pattern of gene activity that was shared only by animals that were monogamous. And they discovered a set of 42 genes whose activity in the brain is strongly associated with monogamy—including genes involved in neural development, learning and memory, and cognition. The results appear in the January 22, 2019, issue of the *Proceedings of the National Academy of Sciences USA*.

"This is surprising because these species have evolved monogamy independently," Young says. "And they've diverged for hundreds of millions of years from one another. So we might expect that because of this evolutionary distance, gene expression in the brain would be quite different. But in fact, we find this shared signature that seems to be related to the mating system of the organism."

Now, those genes may not be setting up entirely new patterns of behavior. They may just be building on underlying mechanisms that all species share, such as pair bonding. "To form a pair bond, one has to tolerate another individual for a long period," Young says.

Yet even members of the most intolerant species have to put up with one another—at least for as long as it takes to mate. Take, for example, shrews. "Shrews tolerate one another for about one day a year," Young says. "So those mechanisms already exist in very aggressive species. But they just happen for short periods." What may happen in monogamous animals is that these conserved pathways, which exist in many different kinds of mating systems, get modified or become more elaborate.

In principle, Young and Hofmann and their collaborators could have extended the study to humans—perhaps by comparing our neural gene expression patterns with those of chimpanzees. But that evaluation might be unfair, given that so much of our courtship behavior is just bananas. SA

Karen Hopkin is a freelance science writer in Somerville, Mass. She holds a doctorate in biochemistry and is a contributor to *Scientific American*'s *60-Second Science* podcasts. This article is adapted from one of her recent podcasts.

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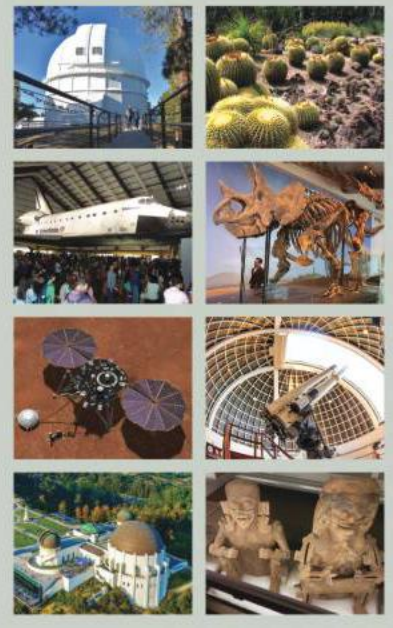

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